

THE JOURNAL OF RAPTOR RESEARCH



VOLUME 28

SEPTEMBER 1994

NUMBER 3

CONTENTS

A SYMPOSIUM ON USING NEST BOXES TO STUDY RAPTORS: DO THE BOXES PROVIDE VIRTUAL REALITY? Frederick R. Gehlbach, Coordinator.....	125
EFFECT OF NEST-BOX SIZE ON NEST-SITE PREFERENCE AND REPRODUCTION IN AMERICAN KESTRELS. Gary R. Bortolotti	127
VALUE OF NEST BOXES FOR POPULATION STUDIES AND CONSERVATION OF OWLS IN CONIFEROUS FORESTS IN BRITAIN. Steve J. Petty, Geoff Shaw and David I. K. Anderson	134
FACTS AND ARTEFACTS IN NEST-BOX STUDIES: IMPLICATIONS FOR STUDIES OF BIRDS OF PREY. Anders Pape Møller	143
SELECTION AND USE OF NEST SITES BY BARN OWLS IN NORFOLK, ENGLAND. Paul N. Johnson	149
NEST-BOX VERSUS NATURAL-CAVITY NESTS OF THE EASTERN SCREECH-OWL: AN EXPLORATORY STUDY. Frederick R. Gehlbach.....	154
THE POST-FLEDGING DEPENDENCE PERIOD OF THE LESSER KESTREL (<i>Falco naumanni</i>) IN SOUTHWESTERN SPAIN. Javier Bustamante and Juan José Negro	158
HABITAT CHARACTERISTICS OF GREAT HORNED OWLS IN SOUTHCENTRAL PENNSYLVANIA. Thomas E. Morrell and Richard H. Yahner	164
PARENT-OFFSPRING RELATIONS DURING THE POST-FLEDGING DEPENDENCY PERIOD IN THE BLACK KITE (<i>Milvus migrans</i>) IN JAPAN. Kimiya Koga and Satoshi Shiraishi	171
HEMATOLOGY AND OCCURRENCE OF HEMOPARASITES IN MIGRATING SHARP-SHINNED HAWKS (<i>Accipiter striatus</i>) DURING FALL MIGRATION. Lauren V. Powers, Mark Pokras, Kim Rio, Cathy Viverette and Laurie Goodrich	178
A RAPTOR ROADSIDE SURVEY IN WESTERN TURKEY AND EASTERN GREECE. Wade L. Eakle	186
SHORT COMMUNICATIONS	
PREPARATION OF AVIAN MATERIAL RECOVERED FROM PELLETS AND AS PREY REMAINS. Beth Ann Sabo and Roxie C. Laybourne	192
USE OF MIST NETS AND A LIVE GREAT HORNED OWL TO CAPTURE BREEDING AMERICAN KESTRELS. Karen Steenhof, George P. Carpenter and James C. Bednarz.....	194
LETTER	197
BOOK REVIEWS Edited by Jeffrey S. Marks	199
IN MEMORIAM: RICHARD R. OLENDORFF, 1943-1994. Robert Lehman	204

The Raptor Research Foundation, Inc. gratefully acknowledges a grant and logistical support provided by Weber State University to assist in the publication of the journal.

Persons interested in predatory birds are invited to join The Raptor Research Foundation, Inc. Send requests for information concerning membership, subscriptions, special publications, or change of address to Jim Fitzpatrick, Treasurer, 14377 117th Street South, Hastings, Minnesota 55033, U.S.A.

The Journal of Raptor Research (ISSN 0892-1016) is published quarterly and available to individuals for \$24.00 per year and to libraries and institutions for \$30.00 per year from The Raptor Research Foundation, Inc., 14377 117th Street South, Hastings, Minnesota 55033, U.S.A. (Add \$3 for destinations outside of the continental United States.) Second class postage paid at Hastings, Minnesota, and additional mailing offices. POSTMASTER: Send address changes to *The Journal of Raptor Research*, 14377 117th Street South, Hastings, Minnesota 55033, U.S.A.

Printed by Allen Press, Inc., Lawrence, Kansas, U.S.A.

Copyright 1994 by The Raptor Research Foundation, Inc. Printed in U.S.A.

THE JOURNAL OF RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

VOL. 28

SEPTEMBER 1994

No. 3

J. Raptor Res. 28(3):125–126

© 1994 The Raptor Research Foundation, Inc.

A SYMPOSIUM ON USING NEST BOXES TO STUDY RAPTORS: DO THE BOXES PROVIDE VIRTUAL REALITY?

FREDERICK R. GEHLBACH, COORDINATOR

Department of Biology, Baylor University, Waco, TX 76798 U.S.A.

Despite the widespread use of nest boxes to study cavity-nesting raptors, investigators have paid scant attention to the naturalness versus artificiality of their findings. Many have not compared life history and population data from nest boxes (experimental treatments) with paired data obtained at natural cavities (presumed controls). In Nero et al. (1987), for example, none of the four contributions employing nest boxes describes the methodology in comparative detail with respect to natural nest sites. This is unfortunate, because nest boxes may or may not be effective in conserving raptors faced with declining natural habitats.

Møller (1989, 1992) and Clobert and Lebreton (1991) have criticized the naturalness of nest-box studies, although some of Møller's observations were rebutted by Koenig et al. (1992). To learn more about this problem, a symposium was held in connection with the joint meeting of the Hawk and Owl Trust and Raptor Research Foundation at the University of Kent, Canterbury, England, in September 1993. The symposium was designed to answer questions about the validity of nest-box versus natural-cavity information in studying owls and kestrels. We hope our contributions will instigate further work wherein appropriate attention is paid to nest-box methods.

The five papers that follow this introduction and one other¹ were presented at the symposium. Gary

Bortolotti gives results of an experimental study showing the effects of nest-box size on reproduction in American kestrels (*Falco sparverius*). Steve Petty, Geoff Shaw, and David Anderson show how nest boxes can be used to study owl populations and a conservation technique in tawny owls (*Strix aluco*) and barn owls (*Tyto alba*). Anders Møller examines possible problems affecting the interpretation of data from nest-box studies. Paul Johnson compares reproduction in barn owls between nest boxes and natural nest sites. Fred Gehlbach tests for differences in nest site choice and reproductive performance between natural nest sites and nest boxes in the eastern screech-owl (*Otus asio*).

Major findings are that boxes were preferred nest sites compared to natural cavities (all species except *O. asio*), boxes did not increase nesting density (except *T. alba*), there was no relationship between box size and either clutch size or fledgling output (*O. asio* and *F. sparverius*), and productivity was the same in boxes and cavities (*O. asio* and *T. alba*).

Nest boxes appear to be adequate substitutes for natural cavities by providing quasi-natural nesting space and unbiased information about population size and productivity. Their general use for studying raptor biology is thus validated. However, we advocate the simultaneous monitoring of box and natural-cavity nests in every study. We conclude that conservationists may replace or rejuvenate cavity-nesting raptor populations by using nest boxes in appropriate foraging habitat.

ACKNOWLEDGMENTS

We greatly appreciate the work of Mike Nicholls in scheduling this symposium, Carl Marti in managing its publication, and Walter Koenig in reviewing the entire copy.

¹ Hubertus Illner's symposium contribution, "Population Changes and Breeding Biology of Little Owls (*Athene noctua*) in Natural Holes and Nest Boxes," will be published elsewhere.

LITERATURE CITED

- CLOBERT, J. AND J.D. LEBRETON. 1991. Estimation of demographic parameters in bird populations. Pages 75–104 in C.M. Perrins, J.D. Lebreton, and G.J.M. Hiron [EDS.], *Bird population studies: relevance to conservation and management*. Oxford Univ. Press, New York, NY U.S.A.
- KOENIG, W.D., P.A. GOWATY AND J.L. DICKINSON. 1992. Boxes, barns, and bridges: confounding factors or exceptional opportunities in ecological studies. *Oikos* 63:305–308.
- MØLLER, A.P. 1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? *Oikos* 56:421–423.
- . 1992. Nest boxes and the scientific rigour of experimental studies. *Oikos* 63:309–311.
- NERO, R.W., R.J. CLARK, R.J. KNAPTON AND R.H. HAMRE [EDS.]. 1987. *Biology and conservation of northern forest owls*. Gen. Tech. Rep. RM-142, Rocky Mountain Forest and Range Exp. Sta., U.S. Forest Serv., Ft. Collins, CO U.S.A.

EFFECT OF NEST-BOX SIZE ON NEST-SITE PREFERENCE AND REPRODUCTION IN AMERICAN KESTRELS

GARY R. BORTOLOTTI

Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada S7N 0W0

ABSTRACT.—I studied American kestrels (*Falco sparverius*) in the boreal forest of northern Saskatchewan from 1988–93. These birds preferred nest boxes over ubiquitous natural cavities. Several lines of evidence, including provisioning of boxes late in the breeding season, suggest that nest boxes did not influence population density. On average, natural cavities had less than one-half the basal area of my standard boxes. The potential effect of box size on nest-site preference and on reproduction was tested in two ways: (1) by offering kestrels a choice between two boxes on the same or nearby tree—one of standard size and one with a 50% smaller basal area, (2) by only having small boxes available in one area. Kestrels strongly preferred the larger boxes, but still chose boxes over cavities when only small boxes were available. Predation rate on nests, clutch size, brood size at fledging, and nest success were all unaffected by box size.

KEY WORDS: *American kestrel; nest box; nest site; population; reproduction.*

Efecto del tamaño de caja anidera sobre el sitio de nidificación y reproducción de *Falco sparverius*

RESUMEN.—Estudí *Falco sparverius* en el bosque boreal del norte de Saskatchewan desde 1988 a 1993. Estas aves prefirieron cajas anideras en vez de cavidades naturales. Las evidencias sugieren que, incluyendo un tardío aprovisionamiento de cajas en la estación reproductiva, las cajas anideras no influyeron la densidad poblacional. En promedio las cavidades naturales tenían menos de un medio del área basal de mis cajas estándar. El efecto potencial del tamaño de las cajas sobre la preferencia por sitio de nidificación y reproducción de *F. sparverius*, fue probado de dos maneras: (1) ofreciendo una elección por dos cajas, una de tamaño estándar y otra de un área basal 50% más pequeña, ubicadas en el árbol o muy cercano a él; (2) ofreciendo solamente de cajas pequeñas en una área. *F. sparverius* prefirió claramente las cajas más grandes. Parámetros como tasa de depredación sobre los nidos, tamaño de la nidada y éxito del nido no fueron afectados por el tamaño de la caja.

[Traducción de Ivan Lazo]

The American kestrel (*Falco sparverius*) breeds in such diverse habitats as deserts, the northern tree-line, agricultural landscapes, and urban areas, spanning a large proportion of the New World (Cade 1982, Bird 1988). Equally impressive is the diversity of natural nest sites used by this species, including cavities in trees, woodpecker holes, ledges of cliffs, holes in earthen banks, and magpie (*Pica* spp.) nests (Cade 1982, Bird 1988). In addition, the array of artificial nest sites includes boxes, drain pipes, chimneys, abandoned buildings and ledges on tall office buildings of big cities (Bird 1988 pers. obs.). A variety of nest sites occurs within a population, not just among locales. The substantial variability among natural nests makes it difficult to address the question of whether nest boxes are unrepresentative of the natural state (see Møller 1989, 1992). To what natural standard should nest boxes be compared?

An investigation of how nest boxes may influence reproduction and population dynamics is still important for a species like the American kestrel. Despite the extensive use of kestrel boxes, there are few data available on consequences of their use. Research should focus on how nest-site parameters influence breeding biology. This would provide much needed information facilitating the comparison of studies in different areas (Møller 1992). My primary objective was to determine how availability and size of boxes may influence population density, nest-site preference and reproduction.

METHODS

Study Area and Population. I studied American kestrels in the vicinity of Besnard Lake, Saskatchewan, Canada (55°N, 106°W), from 1988–1993. The area is boreal forest with an array of forest types and stand ages. The predominant species are trembling aspen (*Populus trem-*

Table 1. Attributes of nest boxes and natural cavities used by American kestrels.

DIMENSIONS	Box ^a		NATURAL CAVITY			
	STANDARD	SMALL	\bar{x}	SD	RANGE	N
Maximum at base (cm)	23.1	16.5	17.0	2.20	14–20	11
Minimum at base (cm)	20.3	14.6	14.7	2.15	14–18	11
Basal area (cm ²)	469	241	198 ^b	45.0	137–254	11
Entrance diameter (cm)	7.5	7.5	7.4 ^c	2.47	5–12	9

^a In addition, all boxes were 37 cm deep from the lid or approximately 25 cm deep from the lower edge of the entrance hole.
^b Derived by the formula for area of a circle or ellipse.
^c Some data were not available because the cavity broke open at the level of the entrance hole when it fell to the ground. If the hole was elliptical, the maximum dimension was used here.

uloides), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), black spruce (*P. mariana*), and birch (*Betula* spp.) all of which grow in pure and mixed-species stands. The mosaic of forest ages and species composition is both natural and human-influenced. The virgin forests were extensively logged for pulpwood in the 1970s and 1980s, with a limited amount of cutting for sawtimber within the last few years. Most forestry operations involved clear-cutting; however, because jack pine was the only commercial species sought, most areas contain clumps of aspens or other species and so there are almost always scattered trees throughout. There is no agriculture or other major land use in the area.

Breeding kestrels prefer openings in the boreal forest, including clearcuts and natural areas such as muskegs, marshes, and burned forest. They are also common where only small clearings exist such as roadways through forests, and in dense brush and saplings 6 m or more tall. They also nest along undisturbed shorelines of lakes surrounded by continuous, dense virgin forests. I did not study a discrete population limited to nest boxes, but sampled part of a large, contiguous population.

In the summer of 1987 and spring of 1988, I erected 153 nest boxes along a gravel highway and logging roads passing through forests and clearcuts. In subsequent years the study was expanded to 345 boxes spanning approximately 300 km of roadway. Each box represents a potential "territory." Most boxes were nailed approximately 4 m above ground for easy access by ladder, and they faced all compass directions. Boxes were put up in all forest types, but were placed usually on aspens as it was in that species that I observed most cavities. The extent of uncut forest around each box varied. Many boxes were placed at the edge of a forest along a roadway, whereas others were put up in lone, mature trees surrounded by young regeneration following a clearcut.

Kestrels arrived on the study area in mid- to late-April. Most eggs were laid over a 4-wk period beginning in mid-May, and the young fledged from mid-July to mid-August. Box occupancy rate varied from 49 to 62% among years. Kestrels migrated from the area in late August and early September.

Attributes of Cavities and Boxes. I obtained too few data for analysis of reproduction in natural cavities, as most nests were situated in dead trees too tall and dan-

gerous to be climbed. Some nesting cavities fell or were cut down, so I measured their interior dimensions at the base and entrance holes (Table 1). All 11 nests were old woodpecker holes, of which eight were situated in trembling aspens, two in birches, and one in a jack pine.

Nest boxes were made from exterior-grade fir plywood 15 mm thick. Their dimensions were determined primarily for efficiency of cutting plywood (Table 1). Lids were hinged for access from above, and most were stained a pale gray (similar to aspen bark) on the exterior to preserve the wood. A few centimeters of wood shavings were placed in the bottom each fall and spring after the box was cleaned out.

Experiments with Availability and Size of Boxes. As a test of whether nest sites were limited in this population, I erected nest boxes late in the breeding season in an area where there was none. I put up 35 boxes 25 May to 2 June 1988 which corresponded to the mid- to late-laying periods. If the study area contained some birds that were capable of breeding, but were prevented from doing so because of limited nest sites (see Bowman and Bird 1987), then these boxes should be occupied.

I chose basal area as the size variable to test given the large differences between cavities and my boxes (Table 1). In addition, studies have shown that clutch size of raptors (Korpimäki 1985) and passerines (e.g., Karlsson and Nilsson 1977) may respond to the basal area of nest boxes. I tested the preference for and consequences of box size in two ways. First I offered kestrels a choice between two boxes. In an area where boxes had already existed for 1–4 yr, I nailed a second, similar box to an adjacent tree, generally a few meters away, at the same height and orientation. When a suitable tree was unavailable, the same nest tree as the old box was used and I placed the new box above or below the old one. Inside one of each pair of boxes, alternating between new and old, I placed an L-shaped plywood insert that reduced the interior dimensions of the box so that it was similar to those of cavities (Table 1). I refer to these modified boxes as small. This experiment was conducted at 71 sites (potential territories) situated along a gravel highway and four logging trails. The distance between adjacent boxes was on average 820 m (SD = 500, N = 58) and the extremes of this portion of the study area were approximately 20 km apart.

A second experiment was conducted in an area of similar

Table 2. Number of active boxes, mean clutch size and success of nest boxes in an area with standard boxes 1988–91 and small boxes 1992–93.

	BOX SIZE					
	STANDARD				SMALL	
	1988	1989	1990	1991	1992	1993
<i>N</i> boxes active/available	10/17	15/17	15/17	15/19	15/19	10/19
Clutch size \bar{x} (SD)	5.1 (0.32)	4.7 (0.46)	4.7 (0.70)	4.7 (0.59)	4.8 (0.44)	4.5 (0.53)
<i>N</i> nests successful/failed	7/3	11/3	13/2	6/9	12/2	3/6

nest-box density and located approximately 40 km from the first. I fitted all existing standard boxes ($N = 19$) with an insert identical to the ones described above. Therefore, there was no choice for box size, and available boxes were similar to the mean size of cavities. My intention was to investigate any changes in reproduction that might be attributed to small boxes compared to the previous 4 years of data collected in this area and on standard boxes elsewhere. I erected new boxes for the choice experiment and installed the inserts in August 1991, and collected data in 1992 and 1993.

Monitoring of Nest Boxes. I visited the boxes approximately every 5–7 d during the pre-laying period. Any whole or partial squirrel nests in the boxes were removed. Adult kestrels were captured on bal-chatri traps or by hand in the nest box. All adults were color-banded and measured upon capture (Bortolotti and Iko 1992). Once eggs were discovered I ceased checking the box until the clutch was complete. I refer to any box that contained eggs or young as being active. The number of eggs laid, hatched, and ultimately the number of young fledged were all documented. Sample sizes are not consistent for all analyses because of missing data, accidents such as trees blowing down, and a loss of road access.

RESULTS

Preference for Boxes and Box Size. Kestrels undoubtedly preferred boxes over natural nest sites, although I did not attempt to find all cavity nests. However, the study area was traversed daily by myself and one or two other field crews and records of all kestrels sighted were kept. Even if all areas between our boxes where kestrels were sighted repeatedly are treated as active natural-cavity sites, which is improbable, then the annual estimate of natural cavity use was only about 5–15%. Color-banding of adults throughout the year helped to confirm the identity of birds using boxes vs. cavities (see also Bortolotti and Iko 1992).

Given that cavities were on average less than half the basal area of the standard nest box (Table 1), size may have been a criterion for nest-site selection. When given a choice between the standard and small

box, eggs were most often laid in the larger box. In 1992, 33 (80.5%) of the 41 boxes with eggs were of standard size, while eight (19.5%) were of the small size ($G = 14.99$, $P < 0.001$). In 1993, only 2 (6%) of 33 clutches were in small boxes ($G = 28.04$, $P < 0.001$).

Size alone is unlikely to explain the selection of boxes over cavities, for there appeared to be no reduction in frequency of box use compared to previous years in the area after all boxes had been converted to the small size (Table 2). The same number of territories were active in 1991 before the experiment, as in 1992 when only small boxes were available. This constancy of occupancy was true for the entire study area as well. In 1993 a reduction in numbers of pairs occurred, but this is consistent with a reduction in use for the entire study area that year. I did not observe pairs at natural cavities in the experimental area in 1993 to account for the difference between years. The consistent use of this area could not be explained by site-tenacity of breeding birds. In 1992 the breeding population of the no-choice experiment was comprised of only 1 of 15 females, and none of 10 males, that had been color-banded as breeders in the area in 1991. Similarly in 1991, when only standard boxes were available, none of 15 females and only one of nine males that nested in the area in 1990, returned to breed there.

Density. Several lines of evidence suggest that natural nest sites were abundant, and the presence of boxes did not increase the density of breeding birds. Even those sites that had been logged contained scattered clumps of mature trees. Woodpeckers, especially the northern flicker (*Colaptes auratus*) and the pileated woodpecker (*Dryocopus pileatus*), were abundant and widely distributed, as were natural cavities in mature trees. Trees immediately adjacent or the nest-box tree itself typically contained apparently suitable cavities. The proximity of con-

secutive boxes along a road was no closer than what I have observed between active kestrel nests under natural conditions.

That boxes were selected over cavities, rather than boxes being the only nest sites available, is also suggested by observations during the pre-laying period. Color-banded male and female kestrels inspected both cavities and boxes within the same territory, and moved among boxes (see Bortolotti and Iko 1992). In some cases, pairs moved from boxes into cavities apparently as a result of disturbance. From 1991–93 in an area far removed from the box-size experiments, I placed electronic balances inside boxes to monitor laying and incubation behavior (see Bortolotti and Wiebe 1993). I installed balances days to weeks prior to laying within territories occupied by kestrels. Eggs were laid in only 26 of 70 boxes with balances. Pairs at the remaining boxes switched over to nearby cavities, or in some cases left the area, probably because of the alteration to the box or the disturbance required to calibrate the equipment. These observations further suggest that kestrels had a choice of nesting in a box or a tree cavity.

It is plausible that the presence of multiple nest sites could influence the attractiveness of the area for breeding kestrels (Hamerstrom et al. 1973). However, this does not appear to be true for the choice experiment. Of the 71 sites available, eggs were laid in 41 (58%) and 33 (46%) boxes in 1992 and 1993, respectively; this rate is comparable to the 58% occupancy in 1991, the only year prior to the experiment for which the same number of potential territories were available in that area.

It does not appear that this population contained individuals that were prevented from breeding for lack of a nest site, for there was no response to the provisioning of boxes late in the nesting season. Only one late box contained eggs, but this was undoubtedly a renesting attempt; the female's brood patches were already refeathering during laying (see Wiebe and Bortolotti 1993). All of the boxes used in this experiment were active in subsequent years, indicating that they were placed in suitable habitat.

The lack of occupancy of the late boxes in 1988 could be accounted for if kestrels avoided newly made boxes, or if prospecting for boxes in a previous year is important as it is for some cavity-nesting waterfowl (Eadie and Gauthier 1985). Neither seems likely for this population. I also erected 41 identical boxes from 19–21 April 1988. These boxes were "early" in that kestrels were just arriving on the

study area. Unlike the late boxes, these early boxes were accepted with a typical occupancy rate (46.3%). Similarly, of 109 "old" boxes, i.e., erected in 1987, 48.8% were active in 1988. Although there were kestrels in the habitat supplied with late boxes, they were likely already committed to a cavity by the time the late boxes became available.

Predation. Predation at kestrel nests was limited to eggs rather than nestlings (Bortolotti et al. 1991) or adults. Depredations were as common in standard boxes (14%) as they were in all small boxes (14%), both years combined. The red squirrel (*Tamiasciurus hudsonicus*) was believed to be largely responsible. These results may not be surprising given that the two box types had the same size of entrance hole (Table 1). Although entrance diameter is usually considered to be relevant to studies of predation, it is not a significant factor here. In this study area there were no large predators, such as raccoons (*Procyon lotor*) that have been problematic in other studies (e.g., Toland and Elder 1987), so any cavity/box entrance big enough for a kestrel was likely big enough for most or all of its egg predators. Also, natural cavities used by kestrels had similar entrance diameters to the nest boxes (Table 1).

Red squirrels, and to a much lesser extent northern flying squirrels (*Glaucomys sabrinus*), may also be competitors for nest sites (see also Balgooyen 1976, Cade 1982, Toland and Elder 1987). Although grassy nests were removed during our visits in the pre-laying period, some were rebuilt and used for rearing young. Squirrels built nests at 31 of a possible 142 sites in the choice experiment over the 2 yr. Grass was found in both boxes at eight sites, in the small box only at 12 sites, and in the standard box only in 11 other sites; therefore, the kestrels' choice of larger boxes was not apparently related to squirrel activity.

Reproduction. There was no apparent relationship between basal area of the box and clutch size (Table 3). The standard boxes of the choice experiment had a mean clutch size of 4.7 eggs (SD = 0.53, $N = 58$) that was the same as all small boxes combined ($\bar{x} = 4.7$, SD = 0.45, $N = 29$). There was no significant difference between the number of large (five and six eggs) and small (three and four eggs) clutches in the standard and small boxes ($G = 0.03$, $P > 0.5$). There also seemed to be no response in clutch size to small boxes in the area where there was no choice when compared among years (Table 2).

Unlike clutch size, the success with which pairs fledged one or more young varied greatly among years (see also Hamerstrom et al. 1973); however, there was still no apparent effect of box size. A comparison of the data for 1988–1993 in the no-choice experiment shows that the 2 yr of small boxes were among the best and worst (Table 2). In the choice experiment of 1992, 22 (67%) of 31 nests in standard-size boxes were successful, while four (50%) of the eight small boxes were successful (Fisher's Exact Test $P = 0.40$). In 1993, nest success over the entire study area was the poorest to date. The two small boxes active in the choice experiment of 1993 became inaccessible shortly after hatching because of a road washing out, and so the only comparison between standard and small is between areas with and without a choice of box size. Only eight (35%) of 23 nests were successful in standard boxes of the choice experiment. Similarly, only three (33%) of nine were successful in the area where there was no choice except small boxes.

The number of young fledged per successful nest also was unaffected by the size of the nest box. In 1992 the three small boxes in the choice experiment fledged four, four, and three young, respectively, while the standard boxes fledged a mean of 3.9 (SD = 1.30, $N = 18$). A mean brood size of 3.9 (SD = 0.96, $N = 15$) was also true for all small boxes of 1992 combined. In 1993, the standard boxes fledged on average 2.1 young (SD = 1.26, $N = 8$), while the three small boxes in the no-choice area fledged one, two and three young, respectively. Collectively, these data do not suggest that box size had any influence on nesting productivity.

DISCUSSION

The American kestrels in this forested region may be different from many of those studied elsewhere in that they appeared to have considerable choice of potential nest sites. The experimental provisioning of boxes late in the season, the abundance of cavities, the presence of many unused nest boxes, and behavioral observations all suggest that these birds had many potential places to breed. Size appeared to be an important criterion for nest-site selection given the preference for standard over small boxes. Kestrels also seemed to prefer the larger of two nest boxes intended for ducks (Gauthier 1988). Oddly, this preference was not associated with any reproductive advantage (e.g., Tables 2 and 3). The effect of box size on reproduction has also been tested on

Table 3. Frequency of clutches of different sizes in nest boxes of different size and experimental treatment 1992 and 1993.

EXPERIMENT	BOX SIZE	CLUTCH SIZE			
		3	4	5	6
Choice	Standard	1	16	40	1
	Small	0	0	6	0
No choice	Small	0	8	15	0

kestrels in captivity with the same negative results (David M. Bird pers. comm.). These findings give support to the validity of comparing nest-box-based studies of kestrels. It is more problematic determining the consequences of the use of boxes versus cavities, and why boxes are so attractive.

To some degree, reproduction of American kestrels in boxes and cavities has been addressed elsewhere. Craig and Trost (1979) and Toland and Elder (1987) found no differences in productivity in a comparison of boxes and natural sites in Idaho and Missouri, respectively. The usual practice by researchers of cleaning out nest boxes, while of concern for some species (Møller 1989), may be unimportant for kestrels. Heintzelman (1971) found that hatching success and nestling survival were not reduced when kestrels used boxes that had not been cleaned after a previous year's use. Similarly, Balgooyen (1976) did not attribute any losses of young to disease and parasites associated with the species' lack of nest sanitation in natural cavities.

The universal effect that provisioning of boxes seems to have is to increase the nesting density of a kestrel population (reviewed by Toland and Elder 1987, Bird 1988). My study may be unusual in that there is no evidence that density increased with nest box use. Similarly, densities did not increase in two species of cavity-nesting owls supplied with boxes (data from this symposium).

A preference of boxes over cavities, even when the latter are available, appears to exist in this and other kestrel populations (Cade 1982, Toland and Elder 1987) and other species (e.g., Brawn 1988). There is no clear explanation for this. Although my standard nest boxes were substantially larger than the cavities kestrels had used (Table 1), size alone cannot account for the strong preference for boxes over natural nests. Kestrels consistently used boxes even when

all available boxes were reduced to a size that made them comparable to cavities (Table 2).

The Saskatchewan kestrels could not have preferred boxes because they themselves were raised in them or had previous successful nesting experience with them. Prior to 1993, my students and I banded over 3300 kestrels. Only about 15% of our color-marked adults have ever been seen again in the years subsequent to their capture. Similar to other kestrel populations (Bowman et al. 1987), less than 3% of the nestlings banded ever returned to breed; therefore, only about 5% of the population each year was comprised of birds that had been reared in boxes.

One attribute of boxes that is unlikely to explain their desirability is their height above ground. Other studies have shown kestrels prefer higher nest sites (Brauning 1983, Toland and Elder 1987). Although I did not measure any heights of cavities, none that I have seen has been as low as my boxes. Usually cavities were two to three times higher than my boxes.

Three remaining variables seem most plausible to explain the box preference of kestrels: dryness, thermal regime, and light levels. Both nest boxes and cavities (see Balgooyen 1976) can be soaked by rain. It would seem likely that natural cavities would, however, be preferred for rain enters the joints of boxes as well as the entrance holes (pers. obs.). The thermal dynamics of the nest site are potentially important, especially in this high-latitude population. Again, however, one might think cavities would be preferred because of the more insulated, thick walls of the nest site. Alternatively, the thin walls of the nest box may allow for rapid solar heating.

The last, and perhaps the most likely, explanation for box preference concerns light levels. Boxes would almost certainly be brighter environments than cavities. Light can enter through the joints of boxes, and perhaps the thinner wall at the entrance hole, relative to that of a cavity, allows for light to reach deeper into the box. Darkness of the nest interior influences box preference in some birds, e.g., European starlings (*Sturnus vulgaris*; Lumsden 1976). Curley et al. (1987) found that active nest boxes of kestrels had significantly higher reflected light levels than those of the same design used by starlings. They suggested that starlings competed more aggressively for dark boxes, rather than kestrels preferring bright ones. However, it is equally plausible that kestrels chose the boxes with more light. Cavities chosen by kestrels to nest in are known to be nonrandom with respect to orientation. It appears that nest sites with

an east-facing direction are often favored (Balgooyen 1976, Raphael 1985). Balgooyen (1976) proposed that such selection had thermal advantages (but see Raphael 1985); however, the directions favored by kestrels would also provide the nest with a maximum amount of sunshine (Curley et al. 1987). A brighter nest interior could have a variety of advantages for parents by giving them better visibility of their eggs and young. I have also seen prey remains in nests, even during times of food shortage, apparently lost in the dark mire that accumulated in the bottom of the box. Higher light levels may reduce food loss, or at least facilitate parents feeding young, offspring self feeding, and perhaps some social interactions.

There are many physical attributes of nest boxes and manners in which the boxes can be made available that may potentially influence reproduction and population dynamics. Testing all of them for a species with such broad natural nesting habits as the American kestrel is problematic. A danger exists in that researchers may become overwhelmed by the variety of alternatives to the point where the study of nest box parameters becomes an end, rather than a means, of investigating meaningful questions in the species' biology. The scope of such research must be limited. Experimental design is thus crucial and depends on the availability of population-specific data. The consequences of artificial nests can only be assessed properly after preliminary data on the behavior and ecology of a population have been collected.

ACKNOWLEDGMENTS

This work was supported by a research grant from the Natural Sciences and Engineering Research Council of Canada, and student support from the Northern Scientific Training Program. I appreciate the cooperation of Saskatchewan Natural Resources for permits. I thank my graduate students K. Wiebe, R. Dawson, and W. Iko, and many field assistants, for their important contribution to the kestrel project. I thank H. Trueman, D.M. Bird, K. Wiebe and R. Dawson for comments on the manuscript.

LITERATURE CITED

- BALGOOYEN, T.G. 1976. Behavior and ecology of the American kestrel (*Falco sparverius*) in the Sierra Nevada of California. *Univ. Calif. Publ. Zool.* 103:1-83.
- BIRD, D.M. 1988. American kestrel. In R.S. Palmer [ED.], *Handbook of North American birds*. Vol. 5. Part 2. Yale University Press, New Haven, CT U.S.A.
- BORTOLOTTI, G.R. AND W.M. IKO. 1992. Non-random pairing in American kestrels: mate choice versus intra-sexual competition. *Animal Behav.* 44:811-821.
- AND K.L. WIEBE. 1993. Incubation behaviour

- and hatching patterns in the American kestrel *Falco sparverius*. *Ornis Scand.* 24:41–47.
- , K.L. WIEBE AND W.M. IKO. 1991. Cannibalism of nestling American kestrels by their parents and siblings. *Can. J. Zool.* 69:1447–1453.
- BOWMAN, R. AND D.M. BIRD. 1987. Behavioral strategies of American kestrels during mate replacement. *Behav. Ecol. Sociobiol.* 20:129–135.
- , J.R. DUNCAN AND D.M. BIRD. 1987. Dispersal and inbreeding avoidance in the American kestrel: are they related? Pages 145–150 in D.M. Bird and R. Bowman [EDS.], *The ancestral kestrel*. Raptor Res. Found. and Macdonald Raptor Res. Centre, Ste. Anne de Bellevue, Que., Canada.
- BRAUNING, D. 1983. Nest site selection of the American kestrel (*Falco sparverius*). *Raptor Res.* 17:122.
- BRAWN, J.D. 1988. Selectivity and ecological consequences of cavity nesters using natural vs. artificial nest sites. *Auk* 105:789–791.
- CADE, T.J. 1982. *The falcons of the world*. Cornell Univ. Press, Ithaca, NY U.S.A.
- CRAIG, T. AND C.H. TROST. 1979. The biology and nesting density of breeding American kestrels and long-eared owls on the Big Lost River, southeastern Idaho. *Wilson Bull.* 91:50–61.
- CURLEY, E.M., R. BOWMAN AND D.M. BIRD. 1987. Nest site characteristics of boxes occupied by starlings and kestrels. Pages 160–164 in D.M. Bird and R. Bowman [EDS.], *The ancestral kestrel*. Raptor Res. Found. and Macdonald Raptor Res. Centre, Ste. Anne de Bellevue, Que., Canada.
- EADIE, J.M. AND G. GAUTHIER. 1985. Prospecting for nest sites in cavity-nesting ducks of the genus *Bucephala*. *Condor* 87:528–534.
- GAUTHIER, G. 1988. Factors affecting nest-box use by buffleheads and other cavity-nesting birds. *Wildl. Soc. Bull.* 16:132–141.
- HAMERSTROM, F., F.N. HAMERSTROM AND J. HART. 1973. Nest boxes: an effective management tool for kestrels. *J. Wildl. Manage.* 37:400–403.
- HEINTZELMAN, D.S. 1971. Observations on the role of nest box sanitation in affecting egg hatchability of wild sparrow hawks in eastern Pennsylvania. *Raptor Res. News* 5:100–103.
- KARLSSON, J. AND S.G. NILSSON. 1977. The influence of nest-box area on clutch size in some hole-nesting passerines. *Ibis* 119:207–211.
- KORPIMÄKI, E. 1985. Clutch size and breeding success in relation to nest-box size in Tengmalm's owl *Aegolius funereus*. *Holarctic Ecol.* 8:175–180.
- LUMSDEN, H.G. 1976. Choice of nest boxes by starlings. *Wilson Bull.* 88:665–666.
- MØLLER, A.P. 1989. Parasites, predators and nest boxes. facts and artefacts in nest box studies of birds? *Oikos* 56:421–423.
- . 1992. Nest boxes and the scientific rigour of experimental studies. *Oikos* 63:309–311.
- RAPHAEL, M.G. 1985. Orientation of American kestrel nest cavities and nest trees. *Condor* 87:437–438.
- TOLAND, B.R. AND W.H. ELDER. 1987. Influence of nest-box placement and density on abundance and productivity of American kestrels in central Missouri. *Wilson Bull.* 99:712–717.
- WIEBE, K.L. AND G.R. BORTOLOTTI. 1993. Brood patches of American kestrels: an ecological and evolutionary perspective. *Ornis Scand.* 24:197–204.

Received 3 December 1993; accepted 10 February 1994

VALUE OF NEST BOXES FOR POPULATION STUDIES AND CONSERVATION OF OWLS IN CONIFEROUS FORESTS IN BRITAIN

STEVE J. PETTY

Forestry Authority, Wildlife Ecology Branch, Ardentinnny, Dunoon, Argyll PA23 8TS, Scotland

GEOFF SHAW

Forest Enterprise, South Scotland Region, 55-57 Moffat Road, Dumfries DG1 1NP, Scotland

DAVID I.K. ANDERSON

Forestry Authority, Wildlife Ecology Branch, Ardentinnny, Dunoon, Argyll PA23 8TS, Scotland

ABSTRACT.—The response of cavity-nesting owls to nest boxes was studied in man-made coniferous forests in northeast England and southwest Scotland. In both study areas field voles (*Microtus agrestis*) were the owls' main food. Voles were abundant on afforested and replanted areas up to 15 yr after planting. Forty territories of tawny owl (*Strix aluco*) were located in one study area prior to 1979. All of these pairs bred in natural sites. In the first year (1980) that nest boxes were available 83% of the population switched to breed in them, and 100% by the fourth year. The number of occupied territories subsequently increased to 66 by 1990, and was attributed to an improvement in food supply resulting from clear-cutting. In another forest, barn owls (*Tyto alba*) declined as abandoned buildings became unavailable due to decay and renovation. The provision of nesting barrels led to a rapid increase in the breeding population, initially by yearlings reared on adjacent farmland. Therefore, nest boxes (barrels) were an essential element in conservation of barn owls in coniferous forests. In contrast to tawny owls, resident barn owls did not switch to nesting barrels. Therefore, in the early years of the study, breeding results may have been biased by a lack of breeding experience in most of the population. The development of an age-structured population took several years.

KEY WORDS: *Barn owl; nest boxes; Strix aluco; tawny owl; Tyto alba.*

Valor de cajas anideras para estudios poblacionales y la conservación de búhos en bosque de coníferas en Bretaña

RESUMEN.—Se estudió la respuesta de búhos, que nidifican en cavidades “naturales,” en relación a cajas anideras ubicadas en plantaciones de coníferas al nor-este de Inglaterra y al suroeste de Escocia. En ambas áreas de estudio *Microtus agrestis* fue la principal categoría alimentaria de los búhos. *Microtus agrestis* fue abundante en áreas desforestadas y reforestadas hasta 15 años después de su plantación. Cuarenta territorios de *Strix aluco* se localizaron en un sitio de estudio hasta 1979. Todas las parejas se reprodujeron en sitios naturales. En el primer año (1980) en el que se dispuso de cajas anideras, el 83% de la población se reprodujo en ellas y el 100% al cuarto año. Subsecuentemente, el número de territorios ocupados se incrementó a 66 en el año 1990, lo que fue atribuido a un mejoramiento en el suplemento alimentario el que a su vez fue resultado del talaje del área. En otro bosque, la población de *Tyto alba* declinó a medida que los edificios abandonados no estuvieron disponibles debido a su destrucción y renovación. La provisión de barriles de nidificación, inicialmente ubicados en terrenos de cultivo adyacente, llevaron a un rápido incremento en las poblaciones reproductivas. Así, las cajas (barriles) fueron un elemento esencial en la conservación de *T. alba* en bosques de coníferas. En contraste a *S. aluco*, individuos de *T. alba* residentes no nidificaron en los barriles. De esta manera, en los inicios del estudio los resultados de reproducción pueden haber estado errados por una falta de experiencia reproductiva en la mayoría de la población. El desarrollo de una población con estructura de edad toma varios años.

[Traducción de Ivan Lazo]

Humans have had a dramatic effect on British forests. Initially this was through deforestation resulting in less than 5% of Britain being forested by 1900. Over the last 75 yr the amount of forest has

increased to about 10%, mainly by planting large coniferous forests in upland regions (Petty and Avery 1990). Such major habitat changes combined with a reduction in persecution have greatly influenced

raptor populations (Newton 1972, 1979, Petty 1988, Petty and Avery 1990).

In this paper we report on studies of tawny owl (*Strix aluco*) and barn owl (*Tyto alba*) in coniferous forests where we have investigated the owls' use of nest boxes. These are the only species of owl to regularly breed in cavities in upland Britain (Petty 1988). The barn owl breeds in large cavities in trees, cliffs, and buildings. The tawny owl is more adaptable, being able to use the abandoned stick nests of ubiquitous species such as carrion/hooded crow (*Corvus corone*) and red and gray squirrels (*Sciurus vulgaris* and *S. carolinensis*) (Cramp 1985). When stick or cavity sites are lacking it can also breed on the ground, typically against the buttress of a tree (Petty 1992a).

Newton (1979) stated that "in any landscape, an upper limit to the number of established raptor pairs is set by food or nest sites, whichever is in shortest supply." These two factors are likely to be the most important for the owls considered in this paper, although we accept that additional factors may also be involved in limiting raptor populations elsewhere.

STUDY AREAS AND METHODS

Study Areas. Tawny owls were studied in 180 km² in the center of Kielder Forest District in northeast England (55°15'N, 2°35'W; Petty 1992a). Prior to afforestation the area was used extensively for sheep grazing. Planting started in 1933 and was largely completed by 1980. Clear-cutting and replanting commenced in 1968 and has been designed to alter spatial patterns within the forest. This is being achieved by shortening and advancing optimum rotation lengths for timber production of 45–55 yr, and felling areas much smaller than the original plantings to create a fine-grained patchwork of different aged trees. Sitka spruce (*Picea sitchensis*) comprised 75% of the forest area, Norway spruce (*P. abies*) 14% and the rest mainly pines and larches.

Barn owls were studied in 490 km² of Newton Stewart Forest District in southwest Scotland (55°00'N, 4°30'W). Before afforestation most of the area was rough grassland, used for sheep grazing. The forest now covers 350 km² with farmland and ungrazed montane habitat comprising the rest. The bulk of the planting, which began in 1934, was carried out in the 1950s and 1960s and was largely complete by the 1980s. The main tree species planted was Sitka spruce (>80%). Clear-cutting and replanting began in 1980, and follows a forest design plan with the same aims as Kielder Forest.

Location of Territories. Occupied tawny owl territories were first located during 1975–78 from pellet/roost stations, nest sites, fledged broods and molted feathers. Erection of nest boxes started in the winter of 1979/80 and subsequently most of the breeding females were caught each time they bred, and, since 1988, most of the males.

Over the years it was possible to determine groups of nest boxes and natural nest sites used by individually known adults. For present purposes each group was considered to form one nesting territory.

Barn owl pairs were located by searching all potential nest sites. Since there were no large cavity-bearing trees in the forest, methods consisted of searching buildings, whether occupied or abandoned. Sightings of birds in the vicinity of a few suitable cliffs were followed up by searching for nests. Searches were carried out in 1970–72 and from 1977 onward, but it was possible to identify nest sites used in earlier years from the accumulation of decayed pellet debris in nest spaces within buildings. Beginning in 1987 most breeding females were trapped each time they bred; a smaller number of males were trapped each year. Many trapped birds were of known age, having been banded as chicks at adjacent farmland nest sites.

Unbanded barn owls were aged by the pattern of feather molt (Cramp 1985, Taylor 1993) as one-year-old (born in the previous year), two-year-old, or older. Tawny owls that were not banded as nestlings were aged by the molt pattern of juvenile regimes and placed into the same age categories as barn owls but with three-year-old as an additional class (Petty 1992a, 1992b).

Occupancy of Territories. Prior to egg laying, each pair of tawny owls would visit several nest sites in their territory. Signs from these visits included traces of down or small body feathers adhering to the entrance hole. These signs occurred up to 1 mo before the eggs were laid. Closer to laying, a deep scrape was formed in the debris at the bottom of the chosen site, usually with down and small body feathers around the edge. In years when pairs did not produce eggs they still went through this process (Petty 1989, 1992a). Nesting territories were classified as occupied when a fresh scrape, with down and/or small body feathers were found in at least one nest site in March–April. Territories were regarded as unoccupied when no signs of owls were found at any nest sites during this period. Tawny owls did not roost in nest sites during the winter (Petty 1992a), so any signs present related to breeding behavior.

Barn owl nest sites showing no fresh signs of owls after 1 April were counted as unoccupied. We had no instances of winter breeding in our study, but in good vole years pairs would sometimes breed into the late summer and early autumn. Buildings were sparsely distributed within the forest at 2–4 km intervals, and most pairs had only one potential nest site. Birds roosted in buildings throughout the year. In spring, occupation was confirmed by flushing the birds, or by the presence of fresh feces, pellets and downy feathers within buildings. Barn owls using tree-mounted nest boxes rarely roosted in them, but visited boxes frequently from mid-winter onward. Occupied boxes had fresh feces and pellets below one or more perches adjacent to the nest box. Prior to egg laying, the female began to roost inside the box and occupancy was confirmed by an accumulation of pellets and small feathers within. Non-laying pairs also conformed to this pattern, particularly during courtship.

Nest Boxes. Tawny owl nest boxes were made from 25-mm-thick, rough-sawn softwood timber, except for the tops which were made from 9-mm-thick exterior grade

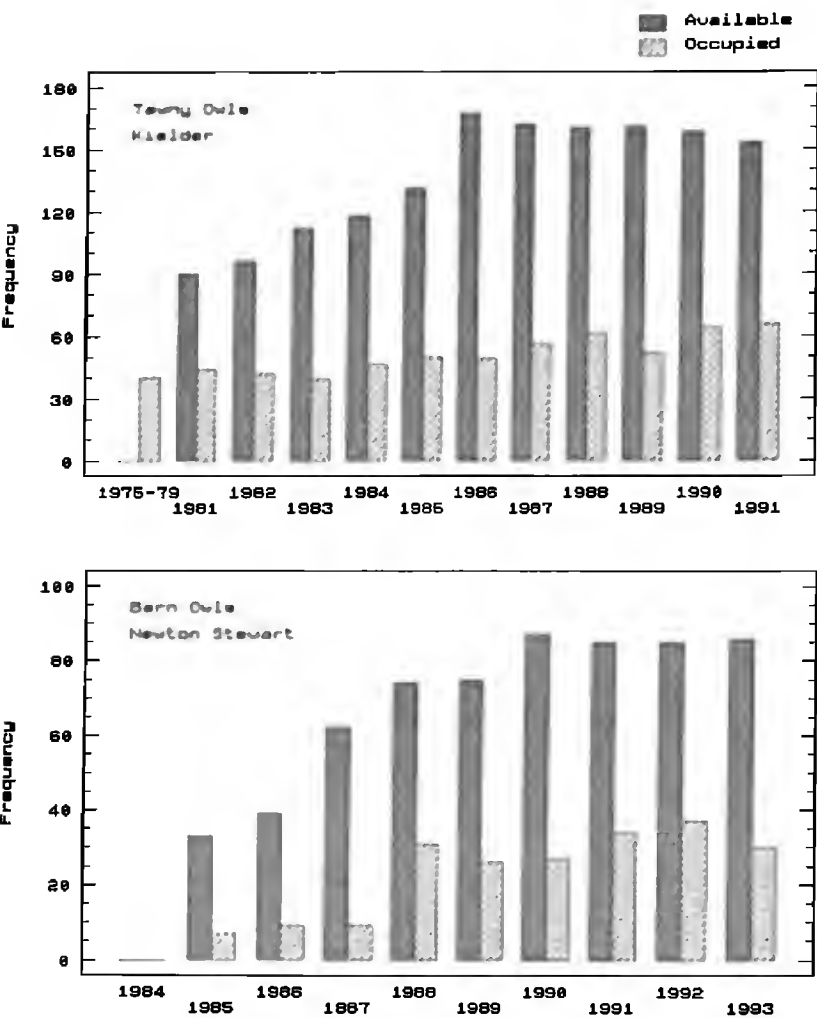


Figure 1. Number of nest boxes available and occupied by tawny owls in Kielder and barn owls in Newton Stewart. Nest boxes were available from 1980 in Kielder and 1985 in Newton Stewart. During 1975–79, tawny owls used natural nest sites; 1980 is excluded because nest boxes were available in only part of the study area. In Kielder, the years 1983, 1986 and 1989 were low vole years.

plywood (Petty 1987a, 1992a). Box exteriors were treated with brown wood preservative. The exterior measurements (mm) were 280 (width of front and back) × 250 (width of sides) × 560 (height), with a square entrance (140 × 150) at the top of the box front. The internal basal area was 340 cm². Inside each box a 100–150 mm layer of dry conifer needles was provided to allow the bird to form a scrape for its eggs. This layer was replaced with new litter after the chicks had fledged. Boxes were fixed to trees at heights of 1.6–5.2 m (but mainly at 3.0–3.5 m) measured from the ground to the base of the box. Boxes were situated to allow the owls a clear flight path into the box and spaced so that one box was available near the center of each of the 40 territories identified during 1975–78, with an additional box between territories and in areas that lacked owls but appeared suitable. This initial placement of boxes resulted in approximately 400 m between boxes along valley systems where the original territories were located. The number of boxes available each year varied because some were moved as areas were clear-felled.

We used three designs of nest boxes for barn owl (Shaw and Dowell 1990). (1) Triangular wooden boxes with

Table 1. Natural and man-made nest sites used by tawny owls in or near to the Kielder study area during 1975–90 and barn owls in the Newton Stewart area during 1975–93.

NEST SITE	TAWNY OWL FREQUENCY (%)	BARN OWL FREQUENCY (%)
Tree hole, enclosed	13 (22.8)	0 (0.0)
Tree hole, open	6 (10.5)	0 (0.0)
Tree crotch, open	3 (5.3)	0 (0.0)
Crow nest	5 (8.8)	0 (0.0)
Goshawk nest	2 (3.5)	0 (0.0)
Cliff ledge	5 (8.8)	0 (0.0)
Ground ^a	10 (17.5)	0 (0.0)
Building (inside)	8 (14.0)	102 (100.0)
Haystack	4 (7.0)	0 (0.0)
Deer high seat ^b	1 (1.8)	0 (0.0)
Total	57 (100.0)	102 (100.0)

^a All sites were at the base of a tree.
^b Elevated platform from which deer are shot.

equal sides of 900 mm and a depth of 320 mm were made of rough-sawn boards 25 mm thick and coated with a wood preservative. An entrance hole (100 × 100 mm) was situated below the frontal apex. (2) Eighty-liter heavy-duty plastic drums, 620 mm high and with an internal diameter of 420 mm, with wooden landing-boards bolted on. The drums were mounted vertically, with a square entrance hole (100 × 100 mm) near the top. (3) The same as design (2) but mounted horizontally with the entrance hole at one end.

To avoid possible competition for nest sites between barn owls and earlier breeding tawny owls, two nest boxes were erected at most sites, 30–80 m apart. A layer of conifer needles or chain saw chips 50–120 mm deep, was provided to facilitate nest scrapes. This layer was renewed annually after successful breeding. The boxes were fixed to trees, 4–6 m high (from ground to box base), situated to allow a clear flight line to the entrance, and were placed adjacent to areas providing good habitat for field voles such as young plantations, rough grasslands and firebreaks. Thirty-three nest box sites were established for barn owls in the winter 1984–85; these were increased to 87 by the end of 1989, after which the number remained constant (Fig. 1).

An important point is that there were far more boxes available each year in both study areas than there were pairs of owls (Fig. 1), ensuring that any increase in the breeding population was quickly detected. All known natural nest sites in both study areas were also checked annually.

Food Supply. Pellet analysis and the identification of prey cached in the nest were used to quantify the main foods of tawny and barn owls (Petty 1987b, 1992a, Shaw unpublished data). In both study areas the main prey of

Table 2. Use of various nest structures (%) by tawny owls in Kielder (1979–84), showing the response of owls to the provision of nest boxes first available for the 1980 breeding season.

NEST SITE	YEAR					
	1979	1980	1981	1982	1983	1984
Nest box	0 (0.0)	15 (83.3)	36 (87.8)	31 (91.2)	10 (100.0)	43 (100.0)
Tree hole, covered	1 (12.5)	2 (11.1)	1 (2.4)	1 (2.9)	0 (0.0)	0 (0.0)
Tree hole, open	2 (25.0)	0 (0.0)	1 (2.4)	1 (2.9)	0 (0.0)	0 (0.0)
Tree crotch, open	1 (12.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Crow nest	0 (0.0)	0 (0.0)	1 (2.4)	0 (0.0)	0 (0.0)	0 (0.0)
Crag ledge	1 (12.5)	0 (0.0)	1 (2.4)	0 (0.0)	0 (0.0)	0 (0.0)
Ground	2 (25.0)	1 (5.6)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Deer high seat	1 (12.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Barn	0 (0.0)	0 (0.0)	1 (2.4)	1 (2.9)	0 (0.0)	0 (0.0)
Total	8 (100.0)	18 (100.0)	41 (99.8)	34 (99.9)	10 (100.0)	43 (100.0)

both owl species was the field vole (*Microtus agrestis*). This rodent feeds largely on grasses, and is most abundant in ungrazed (by domestic animals) grassy habitats such as young conifer plantations (Hansson 1971, Charles 1981, Corbet and Harris 1991). The main grassy habitat within both of our study areas was newly afforested/replanted sites which remained suitable for voles for 12–15 yr after planting.

In Kielder, snap-trapping and vole-sign indices were used to investigate both spatial and temporal changes in vole abundance during 1981–91 (Petty 1992a, Petty and Peace 1993). Populations exhibited a pronounced 3-yr cycle of abundance. Springs with increasing vole abundance occurred in 1981, 1984, 1987, and 1990. Similar trends in vole abundance were observed but not quantified in the barn owl study area until 1989 when vole sign indices were used.

RESULTS

Nest Sites Other Than Nest Boxes. Information on the type of natural and other nest sites (excluding nest boxes) used by tawny owls came from 57 nests located in or near to the Kielder study area during 1975–90 (Table 1). Tree cavities of various types comprised 38.6%, crag and ground nests 26.3%, unused stick nests of other species 12.3%, and man-made structures other than nest boxes 22.8%. These data were probably biased toward the most easily found nests. Crow nests and ground sites used by tawny owls were particularly difficult to locate.

Prior to the erection of nest boxes, barn owls bred exclusively in buildings (Table 1) except for two cliff sites which were used on one and two occasions, respectively, prior to 1975. Twenty-one buildings were confirmed as breeding sites from 1970, but most (62%) of these had been lost, either through dere-

liction (38%) or renovation (24%), and by 1985 only eight remained suitable for barn owls (Shaw and Dowell 1990, Taylor et al. 1992).

Use of Nest Boxes. Boxes for tawny owls were erected for the first time during the winter of 1979–80. In the first year (1980) with boxes available, 83% of the nesting attempts were in boxes, and by 1983 all natural sites in the study area had been abandoned (Table 2). Subsequently (1984–91), only one clutch out of 317 was not laid in a nest box.

Barn owl use of boxes increased from 0–37 pairs during 1985–93 (Fig. 1). A major increase occurred in the 1988 breeding season, following a year when vole populations were increasing. Over the same period the number of nest sites in buildings remained stable at five to six. No suitable buildings were abandoned as breeding sites.

Sector of the Owl Populations Using Nest Boxes. *Tawny owls.* Some females were trapped at natural nest sites to investigate individual responses to nest boxes. Two were caught at ground nests in 1979 and banded. Nest boxes were erected in both territories in November to December 1979. One female switched to breeding in a box in 1980 and for each breeding attempt up to 1991, while the other bred on the ground in 1980 but changed to a box in 1981 and for each breeding attempt up to 1985, after which she died.

Another female was caught at a cliff-ledge site in 1981, probably the one that bred there in 1980, even though a box was available from January 1980. She bred in the box for the first time in 1982 and subsequently up to 1985, after which she died. Other

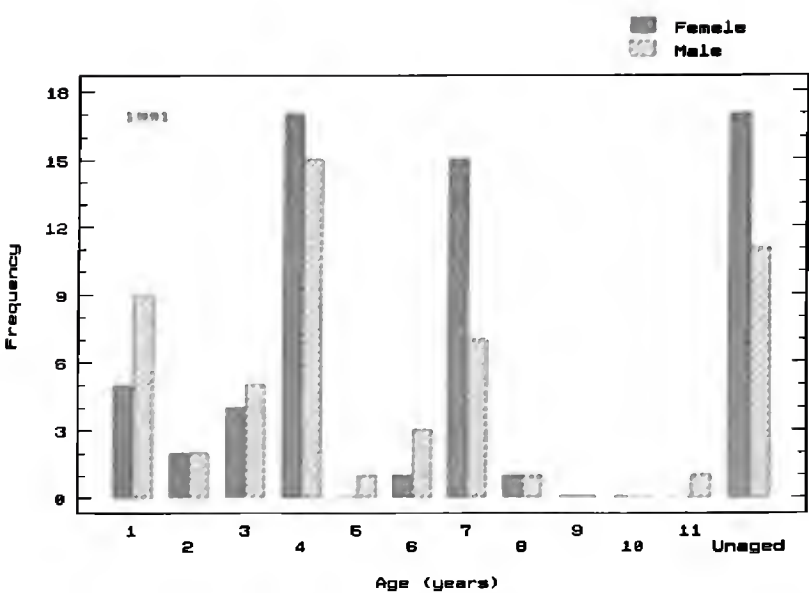


Figure 2. Age structure of breeding male and female tawny owls in Kielder in 1991. One-, four- and seven-yr-old owls were reared in years when vole populations were increasing (see text). The unaged category includes owls caught prior to 1985 before an age determination technique was available, and a few birds caught after 1985 that were too old to be accurately aged (Petty 1992a, Petty 1992b).

females (1986–91) never used the cliff sites, even though at least three ledges on two separate cliffs had been used in the past.

In another territory with two tree holes and a box erected in November 1979, the female bred in the tree hole in 1979 and 1980. In 1981 she used one tree hole followed by the box and then the other tree hole in three nesting attempts, the first two having failed during egg laying. In 1982 she first bred in the box but deserted during incubation and subsequently reared chicks from one of the tree holes. Subsequently, all breeding attempts by this female

and her territorial replacement were in nest boxes even though one of the tree holes was still available in 1991. Thus, the switch to breeding in boxes by tawny owls was achieved by established pairs changing from natural sites.

The age structure of the breeding population exhibited pronounced annual variation, dependent on a pulse of recruitment associated with high productivity and survival of chicks reared in years when vole abundance was increasing (Fig. 2; Petty 1992a). For instance, of the adults that were of a known age in 1991, 82% ($N = 45$) of females and 70% ($N = 44$) of males were from cohorts reared in years when vole abundance was increasing.

Barn owls. Initially, few were trapped at nest boxes (<5), but from 1988 the sample was sufficient to estimate the age structure of the breeding population of females (Table 3). The large increase in occupied nest boxes in 1988 was entirely due to the recruitment of yearling females (81% of breeders). Fewer male owls were trapped, but at 10 newly occupied nest boxes all males were yearlings. The natal origin was known for 18 out of 22 females and seven out of 10 males banded in the previous year as chicks in the local forest and surrounding farmland (Shaw and Dowell 1989). The older females in 1988 had bred in boxes in previous years. Therefore, there was no indication that adult owls already established in buildings switched to breed in nest boxes. This pattern was maintained during 1989–93, when recruitment into the nest box population came from first-time breeders (Table 3).

Because the expansion of the barn owl population breeding in boxes in 1988 was based primarily on a single pulse of recruitment, breeding experience

Table 3. Population age structure (%) of female barn owls breeding in nest boxes in Newton Stewart Forest District, south Scotland, 1988–93.

AGE (YEARS)	YEAR									
	1988		1989		1990		1991		1992	
1	22	(81.5)	8	(40.0)	4	(21.1)	16	(51.6)	10	(47.6)
2	1	(3.7)	9	(45.0)	5	(26.3)	2	(6.5)	3	(14.3)
3	3	(11.1)	1	(5.0)	7	(36.8)	4	(12.9)	0	(0.0)
4	1	(3.7)	2	(10.0)	1	(5.3)	6	(19.4)	2	(9.5)
5	0	(0.0)	0	(0.0)	2	(10.5)	1	(3.2)	4	(19.0)
6	0	(0.0)	0	(0.0)	0	(0.0)	2	(6.5)	0	(0.0)
7	0	(0.0)	0	(0.0)	0	(0.0)	0	(0.0)	2	(9.5)
Mean age (SE)	1.37	(0.16)	1.85	(0.21)	2.58	(0.28)	2.35	(0.30)	2.76	(0.47)
Total	27	(100.0)	20	(100.0)	19	(100.0)	31	(100.0)	21	(99.9)

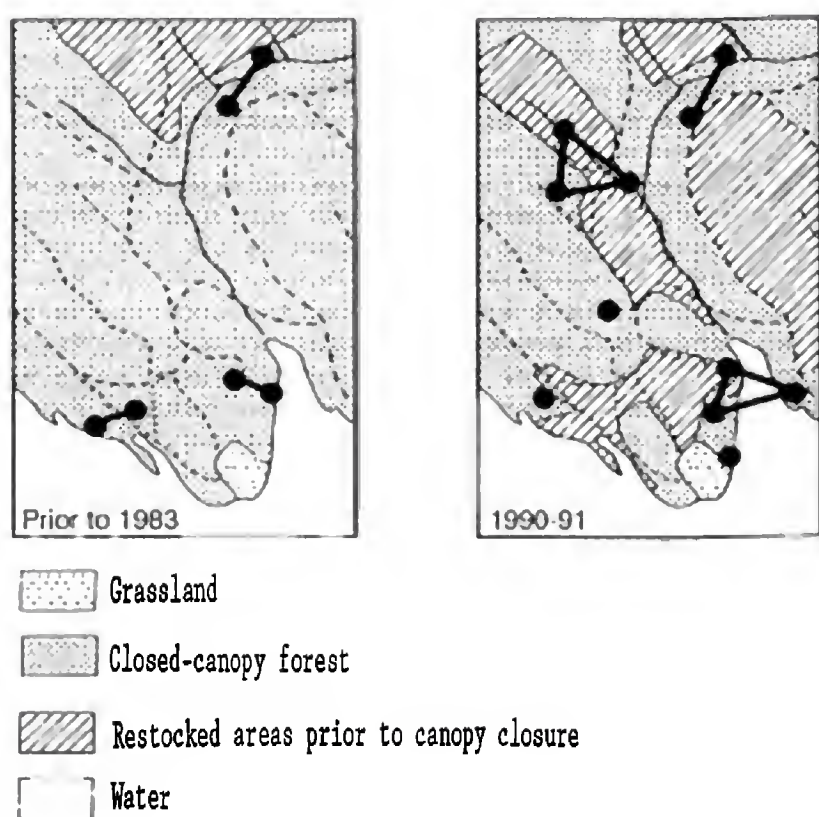


Figure 3. The Plashetts Burn area in Kielder prior to 1983 (left-hand) and in 1990–91 (right-hand). The black circles joined by solid lines show nest sites used by individual pairs of tawny owls. The area measures 2.5×1.5 km.

within the population was initially low. During 1988–93 the mean age and breeding experience of the female owls progressively increased (Table 3).

Influence of Nest Boxes on Owl Density. The annual number of occupied tawny owl territories increased from 40 prior to the erection of nest boxes to 66 in 1991 (Fig. 1). After the provision of nest boxes, this increasing density of tawny owls was related to greater spatial diversity of the habitat, and hence more edge habitat (Petty 1989). This can be demonstrated by comparing two areas of the same size (375 ha) in Kielder (Fig. 3, 4). Prior to 1983, both comprised mostly closed-canopy forest (20–50 yr of age), one area had three pairs of tawny owls and the other had two pairs. By 1990–91 much clear-cutting had broken up the first area and the number of pairs had increased to six (Fig. 3). In the second area, little change occurred during the same period and the number of pairs increased by only one, the additional pair having established near to the only new clear-cut in the area (Fig. 4).

Annual variation in the occupancy of tawny owl territories was also related to field vole abundance (Table 4). In low vole years occupancy averaged 81%, compared to 90–91% in increasing and decreasing vole years.

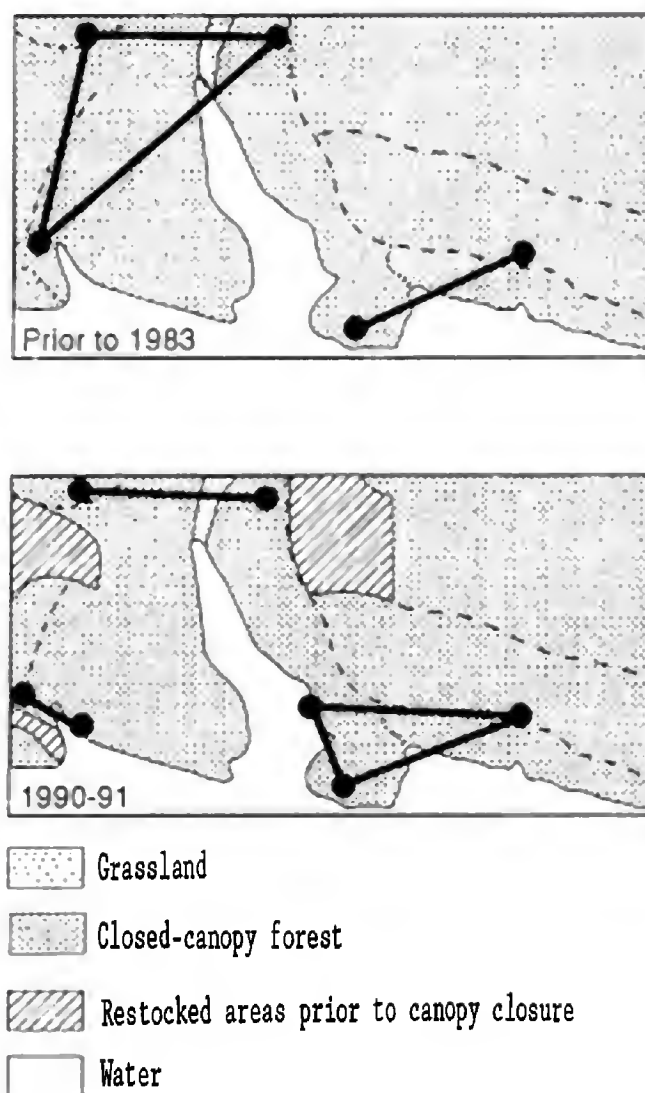


Figure 4. The Belling Burn area in Kielder prior to 1983 (upper) and in 1990–91 (lower). The black circles joined by solid lines show nest sites used by individual pairs of tawny owls. The area measures 1.5×2.5 km.

Barn owl numbers increased primarily due to the availability of nest boxes. Boxes were mainly situated on forest edges and planting breaks, where no major habitat changes were identified during the course of the study. The number of pairs breeding in buildings remained stable, while the pairs based in nest boxes increased from zero, allowing barn owls to exploit small mammal populations in areas where nest sites had previously been absent.

DISCUSSION

Tawny Owls. No work has been done with tawny owls to test experimentally whether nest boxes affect population density. In the present study we consider that boxes had little influence on the increasing owl density. The ultimate reason for the higher owl density was an improved food supply resulting from patchy clear-cutting, producing more vole-rich habitat. This was especially evident between parts of the study area where much clear-cutting occurred

Table 4. Occupancy of tawny owl territories in Kielder (1982–91) in relation to vole abundance.^a

YEARS	VOLE ABUNDANCE	TERRITORIES		TOTAL
		OCCUPIED (%)	UNOCCUPIED (%)	
1983, 1986, 1989	Low	140 (80.5)	34 (19.5)	174
1984, 1987, 1990	Increasing	166 (90.2)	19 (9.8)	184
1982, 1985, 1988, 1991	Decreasing	219 (90.9)	22 (9.1)	241
All years		525 (87.6)	74 (12.4)	599

^a A significantly higher proportion of territories were occupied in years when voles were increasing and decreasing than in low vole abundance years classes ($\chi^2 = 10.22$, $df = 1$, $P < 0.01$).

(Fig. 3) compared with other parts where there was much less (Fig. 4). It was unlikely that the tawny owl population was limited by the lack of nest sites prior to the study, because of the abundance of unused stick nests and potential ground sites. Southern (1970) was also confident that the provision of nest boxes in his study was not responsible for the number of territories increasing from 20–32 during the 10 yr when boxes were available. He attributed the increase to recovery from the severe winter of 1946–47.

In Kielder the whole population switched quickly from natural sites to nest boxes, which suggested that boxes were superior to sites previously used. If so, then tawny owls may be more productive when breeding in boxes. Unfortunately our data from natural sites are largely from earlier years before nest boxes were available; they are not directly comparable to the later data from nest boxes, but show surprisingly little difference in productivity (S.J. Petty unpublished data). However, if the population had still been breeding in natural sites and productivity was lower, the main effect would have been to slow the recorded population increase; the proximate factor most closely associated with increased density was recruitment, of which over 60% came from within the study area (Petty 1992a).

Southern (1970) gave details of the number of nest boxes and the number of pairs of tawny owls using them in his study. In 1950, 2.15 boxes/territory were available, and this had declined to 0.91 boxes/territory by 1959. Overall 55.6% of the nests were in boxes, with no increase in box use during the study. In the first 5 yr, 58.6% of nests were in boxes compared to 52% in the last 5 yr. The reluctance of just under half the population to use nest boxes may have been because the quality of tree holes was good compared to natural nest sites in Kielder.

In broad-leaved woodlands, nest boxes and tree holes are regularly used by both sexes of tawny owls in the winter for roosting. Tawny owls have been recorded roosting in boxes in Wytham Wood, the study area used by Southern (Hirons pers. comm.), in oak (*Quercus* spp.) forests in Belgium (Delmée et al. 1978) and in oak and beech (*Fagus sylvatica*) forests in France (Baudvin and Dessolin 1992). Delmée et al. (1978) also showed that in broad-leaved woodlands the male will often roost in a box near to the nest.

In contrast, tawny owls in coniferous forests do not roost in nest boxes outside the breeding season. If boxes had been used, traces of down and small body feathers would have been present around the entrance hole. P. Saurola (pers. comm.) also found that nest boxes were not used for roosting during the winter in Finland. In winter, coniferous forests may provide sheltered roosting places for tawny owls, whereas broad-leaved woodlands do not, apart from tree cavities or nest boxes. Boxes placed in pairs in a number of territories, in the hope of catching the male roosting in one during the breeding season, failed to attract males in Kielder. This technique had been used successfully by Delmée et al. (1978).

Barn Owls. Nest box provision for barn owls resulted in an increased breeding density. The breeding population expanded in one major pulse by recruiting large numbers of first-time breeders from one cohort (1987; Fig. 1 and Table 3). This initially resulted in a population with a skewed age distribution and a lack of breeding experience unlikely to be encountered in a long-established population. Taylor et al. (1992) reported that first-year females never exceed 40% of a natural barn owl population in the Esk Valley, south Scotland, during 1979–88. The nest box population in the present study resembled the “introduced population” of the model pro-

posed by Taylor and Massheder (1992), where initial colonization was established by the release of a large number of yearling birds.

Many raptors produce fewer young in a first breeding attempt (Newton 1979). In situations where the provision of artificial nest sites has produced a sudden population increase, it should be recognized that the resultant population may initially show an unnatural age structure, and breeding performance may differ from that expected in an established population until a more balanced age structure is achieved through differential survival rates.

The responses of tawny and barn owl populations to nest box provision demonstrates that prior study combined with individual identification is necessary to determine what the effects are of adding nest boxes.

The Validity of Results from Nest Box Studies of Owls. Møller (1989, 1992) has suggested that nest boxes reduce the negative effects of nest predation and ectoparasitism, are often provided at unnaturally high densities, and differ in shape to natural tree cavities. He has argued that together these factors may alter the dynamics of a population compared to one using natural nest sites.

We consider that some of Møller's arguments can be misconstrued when considering cavity-nesting raptors (see also Koenig et al. 1992). Forestry activities, not only in Britain but throughout most of Europe, have had an enormous influence on the structure of woodlands, particularly by the removal of trees with large cavities. Even in seminatural woodlands, the size and frequency of potential nesting cavities are likely to be much reduced through human activities. This may limit breeding density, depending on a species response to alternative nest sites. In addition, when raptors are using natural cavities which vary greatly, it is often difficult to isolate the influence of nest site quality when investigating the effects of other environmental factors on reproduction. Nest boxes allow nest site quality and availability to be standardized therefore reducing the number of variables in such analyses.

Conservation Implications. Tawny owls are well suited to exploit small mammal populations in coniferous forests due to their ability to use a wide variety of nest types, so it is unlikely that nest boxes are essential to maintain breeding populations. In contrast, barn owls are likely to be limited by a lack of large nesting cavities.

Coniferous forests in upland Britain are relatively

young, and although current forest policy stipulates that at least 5% of new plantings should be broad-leaved trees, it will be many years before these produce cavities of a size suitable for barn owls. The broad-leaved trees are for conservation purposes and will not be clear-cut for timber production. So, in the long term they have the potential to provide cavities. Therefore, it is essential that tree species capable of producing large cavities are incorporated. Ash (*Fraxinus excelsior*) and common alder (*Alnus glutinosa*) are particularly valuable and well-suited to many upland sites (Low 1986). In the short term, nest boxes can be used to allow barn owls to exploit vole-rich habitats in the lower valleys of coniferous forests in Britain. As such they allow barn owls to extend their range and breeding density, providing there is a nearby source population to provide recruits.

ACKNOWLEDGMENTS

We are grateful to Forest Enterprise staff in Kielder and Newton Stewart Forest Districts for their cooperation over the years. We also thank Andy Dowell and Iain Taylor for their contribution to the barn owl study, Fred Gehlbach and two anonymous referees for helpful comments on the manuscript, and Diane Chadwick for word processing.

LITERATURE CITED

- BAUDVIN, H. AND J.-L. DESSOLIN. 1992. Analyse de la morphométrie de la Chouettes Hulottes (*Strix aluco*) en Bourgoigne. *Alauda* 60:93-104.
- CHARLES, W.N. 1981. Abundance of the field vole *Microtus agrestis* in conifer plantations. Pages 135-137 in F.T. Last [ED.], Forest and woodland ecology. Inst. Terrestrial Ecol., Cambridge, U.K.
- CORBET, G.B. AND S. HARRIS. 1991. The handbook of British mammals. Blackwell Sci. Publ., Oxford, U.K.
- CRAMP, S. [ED.]. 1985. The birds of the western Palearctic, Vol. IV. Oxford Univ. Press, Oxford, U.K.
- DELMÉE, E., P. DACHY AND P. SIMON. 1978. Quinze années d'observations sur la reproduction d'une population forestière de Chouettes Hulottes (*Strix aluco*). *Le Gerfaut* 68:590-650.
- HANSSON, L. 1971. Habitat, food and population dynamics of the field vole *Microtus agrestis* (L) in south Sweden. *Viltrevy* 8:267-378.
- KOENIG, W.D., P.A. GOWATY AND J.L. DICKINSON. 1992. Boxes, barns and bridges: confounding factors or exceptional opportunities in ecological studies? *Oikos* 63: 305-308.
- LOW, A.J. 1986. Use of broadleaved species in upland forests: selection and establishment for environmental improvement. Forestry Comm. Leaflet 88. Her Majesty's Stationery Office, London, U.K.

- MØLLER, A.P. 1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? *Oikos* 56:421–423.
- . 1992. Nest boxes and the scientific rigour of experimental studies. *Oikos* 63:309–311.
- NEWTON, I. 1972. Birds of prey in Scotland: some conservation problems. *Scot. Birds* 7:5–23.
- . 1979. Population ecology of raptors. T. and A.D. Poyser, Berkhamsted, U.K.
- PETTY, S.J. 1987a. The design and use of a nestbox for tawny owls *Strix aluco* in upland forests. *Q. J. For.* 81: 103–109.
- . 1987b. Breeding of tawny owls *Strix aluco* in relation to their food supply in an upland forest. Pages 167–179 in D.J. Hill [ED.], Breeding and management in birds of prey. Univ. Bristol, Bristol, U.K.
- . 1988. The management of raptors in upland forests. Pages 7–23 in D.C. Jardine [ED.], Wildlife management in forests. Inst. Chartered Foresters, Edinburgh, U.K.
- . 1989. Productivity and density of tawny owls *Strix aluco* in relation to the structure of a British spruce forest. *Ann. Zool. Fenn.* 26:227–233.
- . 1992a. Ecology of the tawny owl *Strix aluco* in the spruce forests of Northumberland and Argyll. Ph.D. dissertation, The Open Univ., Milton Keynes, U.K.
- . 1992b. A guide to age determination of tawny owl *Strix aluco*. Pages 89–91 in C.A. Galbraith, I.R. Taylor and S. Percival [EDS.], The ecology and conservation of European owls. Joint Nature Conservation Committee, Peterborough, U.K.
- AND M.I. AVERY. 1990. Forest bird communities. Forestry Comm. Occas. Paper 26. Forestry Comm., Edinburgh, U.K.
- AND A.J. PEACE. 1993. Temporal and spatial fluctuations in field vole abundance in predator/prey study. Rep. on Forest Research 1992, 40–42. Her Majesty's Stationery Office, London, U.K.
- SHAW, G. AND A. DOWELL. 1989. Breeding by closely related barn owls. *Ringing & Migr.* 10:98.
- AND ———. 1990. Barn owl conservation in forests. Forestry Comm. Bull. 90. Her Majesty's Stationery Office, London, U.K.
- SOUTHERN, H.N. 1970. The natural control of a population of tawny owls (*Strix aluco*). *J. Zool. (Lond)* 162:197–285.
- TAYLOR, I.R. 1993. Age and sex determination of barn owls *Tyto alba*. *Ringing & Migr.* 14:94–102.
- , A. DOWELL AND G. SHAW. 1992. The population ecology and conservation of barn owls *Tyto alba* in coniferous plantations. Pages 16–21 in C.A. Galbraith, I.R. Taylor and S. Percival [EDS.], The ecology and conservation of European owls. Joint Nature Conservation Committee, Peterborough, U.K.
- AND J. MASSHEDER. 1992. The dynamics of depleted and introduced farmland barn owl *Tyto alba* populations: a modelling approach. Pages 105–110 in C.A. Galbraith, I.R. Taylor and S. Percival [EDS.], The ecology and conservation of European owls. Joint Nature Conservation Committee, Peterborough, U.K.

Received 3 December 1993; accepted 18 May 1994

FACTS AND ARTEFACTS IN NEST-BOX STUDIES: IMPLICATIONS FOR STUDIES OF BIRDS OF PREY

ANDERS PAPE MØLLER

Department of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden

ABSTRACT.—Biologists study free-living organisms in order to determine the extent to which they are adapted to their environment (which includes abiotic factors, conspecifics and heterospecifics). Ornithologists have exploited the fact that a number of hole-nesting birds readily breed in nest boxes. Boxes are artificial environments which often reduce the negative effects of nest predation and ectoparasitism, and nest boxes are frequently provided at unnaturally high densities. These aspects of nest-box studies may have important implications for the interpretation of current knowledge of the life history, population dynamics, and ecology of birds because much of the information is derived from nest-box studies. I review the consequences of nest-box studies for the inferences which can be made on bird biology in general and raptor biology in particular. Finally, I suggest ways in which the results obtained from nest boxes can be generalized by quantifying the bias of nest-box studies as compared to studies of the same species breeding in natural cavities.

KEY WORDS: *experimental validity; natural cavities; nest boxes; nest predation; parasitism.*

Realidades y artefactos en estudios de cajas anideras: implicaciones para el estudio de aves de presa

RESUMEN.—Estudios biológicos de organismos silvestres se realizan para determinar la extensión a la que ellos están adaptados al medio ambiente (que incluye factores abióticos, conespecíficos y heteroespecíficos). Los ornitólogos han explotado el hecho de que un gran número de aves que nidifican en cuevas o galerías, se reproducen en cajas anideras. Las cajas son medios ambientes artificiales que a menudo reducen el efecto negativo de la depredación y el ectoparasitismo, además están disponibles en altas densidades, que no necesariamente son naturales. Estos aspectos del estudio de cajas anideras, puede tener importantes implicaciones en la interpretación de conocimientos sobre la historia de vida, dinámica poblacional y ecología de las aves, porque mucha de la información ha sido derivada precisamente de estudios de este tipo. Revisé las consecuencias del estudio de cajas anideras respecto a las inferencias que podrían ser hechas sobre la biología de aves en general y sobre la biología de rapaces en particular. Finalmente, sugiero maneras en las que los resultados obtenidos de estos estudios podrían ser generalizados, cuantificando el error que se obtiene al comparar con estudios de la misma especie que se reproducen en cavidades naturales.

[Traducción de Ivan Lazo]

Current knowledge of the biology of birds is vast compared to that of many other classes of organisms, and this is mainly due to the immense interest in birds and the ease with which bird studies are performed. A large amount of information on avian biology can be attributed to the success of nest-box studies, and areas of research influenced by these studies include population regulation, life history evolution, quantitative genetics, sexual selection, and reproductive physiology. Many of the results have been included in textbooks and form the basis for generalizations on bird biology.

Ornithologists put up nest boxes for the joy and pleasure of having breeding birds around, the wish to enhance population size and reproductive success of cavity-nesting birds, and the ease at which bio-

logical studies can be performed on birds in nest boxes. If the objective of using nest boxes is the second, or particularly the third, mentioned above, there are reasons to plan the study carefully, because nest boxes differ from natural cavities in a number of different ways, and this affects predation risks and infestations with parasites, and therefore potentially a number of reproductive parameters (Møller 1989, 1992). Most individuals of cavity-nesting species breed in natural holes and it is likely that they are adapted to this environment. Individuals breeding in nest boxes mainly originate from the fraction of the population breeding in natural cavities, and this may make tests of adaptive hypotheses difficult by relying entirely on populations breeding in nest boxes.

I briefly review (1) the effect of nest boxes on the probability of nest predation and ectoparasite infestations, (2) the effect of nest-box density on reproduction and interspecific relationships, and (3) the relationship between features of nest-box design and avian reproduction. This is done by relying extensively on the vast literature on hole-nesting birds including that on raptors.

COMPARISON OF NEST BOXES AND NATURAL CAVITIES

Nest Predation. Nest predation is one of the most important determinants of the reproductive success of birds (Ricklefs 1969). Cavity-nesting birds have been supposed to suffer less often than open-nesting species (Lack 1954, Nice 1957, Ricklefs 1969, Korpimäki 1984, Sonerud 1985), but this apparent difference is due to low nest-predation estimates obtained from nest-box studies. A Swedish study of seven different cavity-nesting passerine birds revealed on average 62% lower mortality due to predation in boxes as compared to natural cavities (Nilsson 1984), and similar results have been obtained elsewhere (Korpimäki 1984, Lundberg and Alatalo 1992). Unbiased estimates of nest predation on hole-nesting birds breeding in natural cavities do not suggest that the predation rate is any lower than in open-nesting species breeding under similar environmental conditions (Nilsson 1986).

Nest predation rates may depend on the intensity of begging calls of offspring as mediated by their hunger level (Skutch 1976). Offspring raised under poor environmental conditions (in poor habitats, outside the main breeding season, or by parents of low phenotypic quality) may suffer from predation more often than others. The use of nest boxes and the resultant reduction in nest predation is therefore likely to particularly improve the reproductive success of individuals of poor phenotypic quality (e.g., young birds from poor habitats of low competitive ability).

Nest predation may be relatively less important for birds of prey breeding in nest boxes, because these species are able to efficiently defend the box against predators. However, mammalian predators are sometimes important in boxes inhabited by owls (Sonerud 1985). The extent to which nest-predation rates of birds of prey differs between boxes and natural cavities has not been quantified (but see Korpimäki (1984) for a preliminary study).

The effective elimination of nest predation from

boxes may affect nest site choice of females (Alatalo et al. 1986) and increase the overall reproductive success of birds, particularly of individuals of low phenotypic quality. Reproductive strategies of birds have been suggested to be influenced by nest predation (e.g., Slagsvold 1982, Lundberg 1985, Lima 1987), and the reproduction of birds breeding in predator-safe boxes may be severely affected by the absence of any predation risk. Tawny owls (*Strix aluco*) at some locations in Britain prefer nest boxes and have abandoned natural sites entirely (Petty et al. 1994).

Ectoparasitism. Ectoparasitism may play an important role in the life of birds, and affects aspects as diverse as reproduction, interspecific interactions, and sexual selection (Price 1980, Price et al. 1988, Hamilton and Zuk 1982, Loya and Zuk 1991). Ectoparasites are common inhabitants of cavity nests, and a number of experimental studies have demonstrated severe negative effects on reproductive performance (review in Møller et al. 1990). The high virulence of ectoparasites of hole-nesting birds may be due to their frequent horizontal transmission to other conspecific host individuals. Horizontal transmission is likely to increase the virulence of parasites while vertical transmission generally selects for reduced virulence (Ewald 1980). Old nests and their contents have traditionally been removed from nest boxes, even though this procedure has not been reported in publications (Møller 1989, 1992). Scientists using nest boxes as a tool have repeatedly explained to me, when asked why they removed old nests from their boxes, that nest removal was adopted because ectoparasites were a nuisance to birds and field assistants! Nest removal may have resulted in substantial reductions in ectoparasite loads of nest boxes compared to that of natural cavities.

Ectoparasites have a number of detrimental effects on bird hosts. These effects include reduced attractiveness of potential nest sites, delayed reproduction, increased mortality, reduced growth rate, premature fledging, and reduced future reproductive potential (e.g., Moss and Camin 1970, Brown and Brown 1986, Møller 1993). Ectoparasites are frequent vectors of diseases (e.g., Price 1980, Marshall 1981), and reductions in ectoparasite loads may reduce the probability of disease transmission.

The effects of parasite abundance on reproductive performance have been assessed experimentally in a number of bird species. One interesting finding is that the same ectoparasite species may have dra-

matically different virulence in different populations of the same host species (Richner et al. 1994a, 1994b, K. Allander and R. Dufva unpubl. data). This result suggests that it is difficult to make any generalizations from one study to another, even when the same host and parasite is involved.

There is no information available on differences between boxes and natural cavities for raptor ectoparasite infestations, but the removal of debris and, hence, parasites from nest boxes may reduce the variance in reproductive success of hosts, particularly due to improved reproductive performance of host individuals of poor phenotypic quality (Møller et al. 1993). Raptors may also suffer from horizontal transmission of virulent parasites from prey, particularly in natural nest sites where prey remains are left behind.

Population Density. This feature has been hypothesized to affect a number of reproductive variables such as the timing of reproduction, clutch size, and reproductive failure (Lack 1954, 1966). The direct effect of population density has only been verified experimentally in a few cases (Lundberg and Alatalo 1992), although the amount of circumstantial evidence is considerable. Most nest-box studies are characterized by higher population densities than in surrounding areas without boxes (e.g., Marti et al. 1979, Ziesemer 1980). Population density is known to affect the intensity of both intraspecific and interspecific interactions (e.g., Lundberg and Alatalo 1992). Density-dependent intraspecific competition may account for some of the reductions in reproductive success at high densities, but this effect will depend on whether birds breed in natural cavities or boxes. Provisioning of boxes has been shown to result in dramatic increases of local population density of birds (von Haartman 1971) including raptors (Marti et al. 1979), perhaps severely increasing the intensity of intraspecific competition. Density-dependent nest predation has been reported from one study of nest-box breeding tits (Dunn 1977). The intensity and the prevalence of ectoparasitism are density-dependent in a number of cases (review in Møller et al. 1993). Ectoparasites particularly have detrimental effects on their hosts during poor environmental conditions (Møller et al. 1993); for example, at high population densities. The reproductive success of hosts breeding in nest boxes may therefore particularly be improved at high population densities when hosts otherwise are severely negatively affected by parasitism.

The negative effects of nest predation, ectoparasitism, and population density may interact synergistically in a number of different ways. The effects of interspecific interactions may be particularly severe under high population densities, because resource abundance per individual is low. The effects of nest predation may also be aggravated under high levels of ectoparasitism, because parasite infestation may increase the level of hunger and the begging intensity of offspring. Interaction effects on reproduction are likely to be reduced in nest-box studies, where the level of parasitism and the risk of nest predation are low.

Design of Nest Boxes. The size of cavities affects the frequency of occupation in a number of different bird species, including raptors (e.g., van Balen 1984, van Balen et al. 1982, Rendell and Robertson 1989, Bortolotti 1994). Cavity size and location affect predation risk (e.g., Lundberg and Alatalo 1992), and settlement by prospective breeders may therefore depend on the phenotypic quality of individuals. Low quality individuals may be unable to get access to preferred natural nest sites and be forced to accept nest boxes of lower quality. Alternatively, nest-box dimensions may exceed what is available in the environment, and a small number of nest boxes may result in primarily high quality individuals settling in boxes.

A second feature of some cavity-nesting species, including raptors, is that reproductive parameters appear to be adjusted to the size of the cavity (e.g., Karlsson and Nilsson 1977, van Balen 1984, Korpimäki 1985, Bortolotti 1994). One study has reported a causal relationship between cavity size and clutch size in tits (Löhrl 1973). It is also possible that birds may be able to assess the risk of nest predation as determined by the features of the nest cavity and adjust reproductive investment to perceived risks (see Sonnerud (1985) for a case of nest site choice in Tengmalm's owl *Aegolius funereus*). The reproductive success of birds breeding in nest boxes can therefore directly be influenced by the size of boxes provided, and the features of nest boxes should preferably reflect what is available in natural cavities, if scientists intend to make inferences about the adaptive nature of reproductive decisions.

CONCLUSIONS

The points raised in this paper may appear to be of minor importance compared to the amount of information gained from large-scale population

studies using boxes (Koenig et al. 1992). This conclusion is premature, because most current studies of cavity-nesting bird species address ecological and micro-evolutionary questions with the hidden assumption that birds are able to utilize the situation in nest boxes in the same way as natural sites. For example, scientists have for several decades studied optimal clutch size in hole-nesting birds by relying entirely on birds breeding in nest boxes, that exclude or reduce important causes of nest failure. However, the assumption of comparable responses in natural nest sites and in boxes has not been rigorously tested and this gives rise to a host of validity problems.

Experimental studies usually consider four different types of validity, viz. statistical conclusion validity, internal validity, construct validity, and external validity (e.g., Cochran and Cox 1957). There may not be a high degree of statistical conclusion validity in nest-box studies if there is no covariation between two or more variables of interest. The internal validity may also be low if there is a lack of standardization of treatments within and between subjects, as would be the case if a particular kind of bird such as competitively superior individuals are attracted to predator-safe nest boxes. There may also be problems with construct validity which relates to the cause and effect constructs involved in the relationship. For example, if the effect of population density on reproduction is studied in a nest-box experiment, there may be other differences between plots than differences in density; for example, if a larger proportion of low quality individuals breed in boxes provided at a high density. Finally, nest-box studies may suffer from problems with external validity, because it is impossible to generalize a probably causal relationship across individuals, times and settings (natural cavities and boxes). External validity may be reduced because of interactions between selection and treatment if a particular kind of individual is attracted at high population densities, because of interactions between settings and treatment (population density is higher in nest-box plots), and because of interactions between history and treatment (individuals that have previously bred in boxes may preferentially settle in high density plots).

RECOMMENDATIONS

The current knowledge of birds is to a large extent due to studies of hole-nesting species. Scientists have exploited the opportunity to obtain information on

large numbers of individual birds throughout their lives by providing nest boxes. My criticism is not an attempt to discard previous knowledge but to encourage better nest-box studies in order to validate the results of previous studies. This can be done by following a number of simple recommendations.

First, it is very important that scientists report exactly what has been done in a particular study. Only detailed knowledge of what was done will allow comparison of results from studies in different sites. A brief list of questions includes the following: What was the size of boxes and the size of the entrance hole? Were new boxes provided annually? Were old nests or nest-box debris removed? What was the density of boxes?

Second, nest-box size and the size of entrance holes have been found to affect occupancy and various life history characters. This problem can be handled in two different ways. Nest boxes with mean dimensions resembling those of natural cavities occupied by the species can be provided. Alternatively, the experimenter may in a pilot study provide boxes of a range of different sizes and record the response of the species to variation in box size and the size of entrance holes.

Third, it is essential for all nest-box studies that comparisons are made between reproductive parameters in nest boxes and in natural cavities. This has now been done in a number of species (e.g., Korpimäki 1984, Robertson and Rendell 1990, Lundberg and Alatalo 1992, Bortolotti 1994, Gehlbach 1994), and many studies have reported increased mean and/or reduced variance in reproductive success in boxes. Assessment of reproduction in boxes versus natural cavities could preferentially be made in a pairwise design which controls for differences in environmental conditions (Gehlbach 1994). This will allow conclusions about the extent to which observations from boxes are comparable to those from natural cavities.

ACKNOWLEDGMENTS

F.R. Gehlbach kindly provided constructive criticism. I thank the Swedish Natural Science Research Council for support.

LITERATURE CITED

- ALATALO, R.V., A. LUNDBERG AND C. GLYNN. 1986. Female pied flycatchers choose territory quality and not male characteristics. *Nature (Lond.)* 323:152-153.
- BORTOLOTTI, G.R. 1994. Effects of nest-box size on nest-

- site preference and reproduction in American kestrels. *J. Raptor Res.* 28:127–133.
- BROWN, C.R. AND M.B. BROWN. 1986. Ectoparasitism as a cost of coloniality in the cliff swallow (*Hirundo pyrrhonota*). *Ecology* 67:1206–1218.
- COCHRAN, W.D. AND G.M. COX. 1957. Experimental design. Wiley, New York, NY U.S.A.
- DUNN, E.K. 1977. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. *J. Anim. Ecol.* 46:633–652.
- EWALD, P.W. 1980. Evolutionary biology and the treatment of signs and symptoms of infectious disease. *J. Theor. Biol.* 86:169–176.
- GEHLBACH, F.R. 1994. Nest-box versus natural-cavity nests of the eastern screech-owl: an exploratory study. *J. Raptor Res.* 28:154–157.
- HAMILTON, W.D. AND M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387.
- KARLSSON, J. AND S.G. NILSSON. 1977. The influence of nest-box area on clutch size in some hole-nesting passerines. *Ibis* 129:243–258.
- KOENIG, W.D., P.A. GOWATY AND J.L. DICKINSON. 1992. Boxes, barns, and bridges: confounding factors or exceptional opportunities in ecological studies. *Oikos* 63:305–308.
- KORPIMÄKI, E. 1984. Clutch size and breeding success of Tengmalm's owl *Aegolius funereus* in natural cavities and nest boxes. *Ornis Fenn.* 61:80–83.
- . 1985. Clutch size and breeding success in relation to nest-box size in Tengmalm's owl *Aegolius funereus*. *Holarct. Ecol.* 8:175–180.
- LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford, U.K.
- . 1966. Population studies of birds. Clarendon Press, Oxford, U.K.
- LIMA, S.L. 1987. Clutch size in birds: a predation perspective. *Ecology* 68:1062–1070.
- LÖHRL, H. 1973. Einfluss der Brutraumfläche auf die Gelegegröße der Kohlmeise. *J. Ornithol.* 114:339–347.
- LOYE, J.E. AND M. ZUK [EDS.]. 1991. Bird-parasite interactions: ecology, evolution, and behaviour. Oxford Univ. Press, Oxford, U.K.
- LUNDBERG, A. AND R.V. ALATALO. 1992. The pied flycatcher. T. & A.D. Poyser, London, U.K.
- LUNDBERG, S. 1985. The importance of egg hatchability and nest predation on clutch size evolution in altricial birds. *Oikos* 45:110–117.
- MARSHALL, A.G. 1981. The ecology of ectoparasitic insects. Academic Press, London, U.K.
- MARTI, C.D., P.W. WAGNER AND K.W. DENNE. 1979. Nest boxes for the management of barn owls. *Wildl. Soc. Bull.* 7:145–148.
- MØLLER, A.P. 1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? *Oikos* 56:421–423.
- . 1992. Nest boxes and the scientific rigour of experimental studies. *Oikos* 63:309–311.
- . 1993. Ectoparasites increase the cost of reproduction in their hosts. *J. Anim. Ecol.* 62:309–322.
- , K. ALLANDER AND R. DUFVA. 1990. Fitness effects of parasites on passerine birds: a review. Pages 269–280 in J. Blondel, A. Gosler, J.D. Lebreton, and R. McCleery [EDS.], Population biology of passerine birds: an integrated approach. Springer-Verlag, Berlin, Germany.
- , R. DUFVA AND K. ALLANDER. 1993. Parasites and the evolution of host social behavior. *Adv. Study Behav.* 22:65–102.
- MOSS, W.W. AND J.H. CAMIN. 1970. Nest parasitism, productivity, and clutch size in purple martin. *Science* 168:1000–1003.
- NICE, M.M. 1957. Nesting success in altricial birds. *Auk* 74:305–321.
- NILSSON, S.G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis Scand.* 15:167–175.
- . 1986. Evolution of hole-nesting in birds: on balancing selection pressures. *Auk* 103:432–435.
- PETTY, S.J., G. SHAW AND D.I.K. ANDERSON. 1994. Value of nest boxes for population studies and conservation of owls in coniferous forests in Britain. *J. Raptor Res.* 28:134–142.
- PRICE, P.W. 1980. Evolutionary biology of parasites. Princeton Univ. Press, Princeton, NJ U.S.A.
- , M. WESTOBY AND B. RICE. 1988. Parasite-mediated competition: some predictions and tests. *Am. Nat.* 131:544–555.
- RENDELL, W.B. AND R.J. ROBERTSON. 1989. Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities. *Condor* 91:875–885.
- RICHTER, H., A. OPPLINGER AND P. CHRISTE. 1994a. Effect of an ectoparasite on reproduction in great tits. *J. Anim. Ecol.* (in press).
- , P. CHRISTE AND A. OPPLINGER. 1994b. Ectoparasites affect timing of breeding in the great tit (*Parus major*). *Behav. Ecol.* (in press).
- RICKLEFS, R.E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* 9:1–48.
- ROBERTSON, R.J. AND W.B. RENDELL. 1990. A comparison of the breeding ecology of a secondary cavity-breeding bird, the tree swallow (*Tachycineta bicolor*) in nest-boxes and natural cavities. *Can. J. Zool.* 68:1046–1052.
- SKUTCH, A.F. 1976. Parent birds and their young. Texas Univ. Press, Austin, TX U.S.A.
- SLAGSVOLD, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* 54:159–169.
- SONERUD, G. 1985. Nest-site shift in Tengmalm's owl *Aegolius funereus* as defense against predation involving

- long-term memory in the predator. *J. Anim. Ecol.* 54: 179–192.
- VAN BALEN, J.H. 1984. The relationship between nest-box size, occupation and breeding parameters of the great tit *Parus major* and some other hole-nesting species. *Ardea* 72:163–175.
- , C.J.H. BOOY, J.A. VAN FRANEKER AND E.R. OSIECK. 1982. Studies on hole-nesting birds in natural nest sites. 1. Availability and occupation of natural nest sites. *Ardea* 70:1–24.
- VON HAARTMAN, L. 1971. Population dynamics. Pages 391–459 in D.S. Farner and J.R. King [Eds.], *Avian biology*. Vol. 1. Academic Press, New York, NY U.S.A.
- ZIESEMER, F. 1980. Siedlungsdichte und Bruterfolg von Schliereulen (*Tyto alba*) in einer Probestfläche vor und nach dem Anbringen von Nisthilfen. *Vogelwelt* 101: 61–66.

Received 3 December 1993; accepted 18 July 1994

SELECTION AND USE OF NEST SITES BY BARN OWLS IN NORFOLK, ENGLAND

PAUL N. JOHNSON

*The Durrell Institute of Conservation and Ecology, The University, Canterbury,
Kent CT2 7NX United Kingdom*

ABSTRACT.—Between 1989 and 1993 reproduction was monitored at 96 barn owl (*Tyto alba*) breeding sites in England. Nests were located in tree cavities, buildings, and nest boxes in farm buildings and mature trees. Many of the sites other than nest boxes used by owls were of human origin, but the number of those declined during the course of the study due to deterioration of human-made structures and competition from other species. Nest boxes increased the population density from 15 breeding pairs/100 km² to 27 pairs. Over the study period, pairs using nest boxes produced significantly larger clutches than at other sites, but the number of fledglings was not significantly different among types of nest sites.

KEY WORDS: *barn owl; breeding ecology; England; human-altered habitats; nest boxes; Tyto alba.*

Selección y uso de sitios de nidificación por *Tyto alba* en Norfolk, Inglaterra

RESUMEN.—Entre 1989 y 1993 se monitoreó la reproducción en 96 sitios reproductivos de *Tyto alba*. Los nidos se localizaron en cavidades de árboles, edificios, cajas anideras en construcciones agrícolas y árboles maduros. Mucho de estos sitios, aparte de las cajas anideras, usados por *T. alba* fueron de origen humano, pero el número de ellos declinó durante el curso del estudio debido al deterioro de las estructuras artificiales y a la competencia con otras especies. Las cajas anideras incrementaron la densidad poblacional de 15 parejas reproductivas/100 km² a 27 parejas. En el período de estudio, las parejas que usaron las cajas anideras produjeron nidadas significativamente más grandes que en otros sitios, pero el número de volantones no fue significativamente diferente entre los distintos tipos de sitios.

[Traducción de Ivan Lazo]

The barn owl (*Tyto alba*) is currently classified as vulnerable in northwest Norfolk, England by Shawyer (1987) who recorded a 66% decline to just 82 breeding pairs and a density of 2.9 pairs per 100 km² from the 240 pairs and 8.4 pairs per km² recorded by Blaker (1933). A survey of this area found that 60% of the barn owl population used natural tree cavities for nesting (Johnson 1991). Regional trends in the type of nesting site selected by a barn owl population have been reported in Bunn et al. (1982).

Artificial nesting sites have been readily used by owls and have been widely used in long-term studies of owls (Southern 1959, 1970, Korpimäki and Sul-kava 1987, Saurola 1989). By providing nest boxes, the breeding population densities of owls were increased above the levels previously thought to be limited by the availability of natural sites. Lenton (1978) demonstrated that the breeding density of previously rare barn owls in Malaysia could be increased with the provision of nest boxes. On the other hand, the naturalness of results obtained from nest-

box studies has been criticized by Møller (1989, 1992).

The primary objectives of this study were to monitor and compare reproductive levels between natural and nest-box breeding sites, and to promote a sustainable expansion of breeding barn owls by extending the range and number of nesting site types.

METHODS

The study area (10 × 15 km) was intensively farmed in individual units ranging from 300–15 000 ha. Principle crops were winter and spring cereals, sugarbeets, and rough grassland.

Nest sites were located during 1989–90 by methodically searching all possible structures, interviewing landowners, and by following birds to their nest sites. The locations of all potential natural nesting sites were recorded, together with details of their dimensions.

Nest boxes placed in buildings ($N = 43$) were constructed from 8 mm exterior grade plywood and located in suitably safe and quiet sites on every farm within the study area. Tree-mounted nesting boxes ($N = 17$) were made from 19 mm exterior grade plywood for increased thermal insulation because this species is known to be sensitive to extreme cold (Johnson 1974). Tree-mounted

Table 1. Reproduction by barn owls at four nest site types in Norfolk, England. Tabular values are percentages or mean \pm 1 SD. Numbers of nest types are in parentheses.

REPRODUCTIVE PARAMETERS	NEST SITE TYPES			
	TREE BOX (8)	BUILDING BOX (43)	TREE CAVITY (28)	BUILDING (14)
Percent of site use	29.4	25.6	57.1	10.6
Clutch size	5.4 \pm 1.8	5.0 \pm 1.4	4.3 \pm 1.3	3.9 \pm 1.1
Brood size	4.1 \pm 1.7	3.7 \pm 1.2	3.3 \pm 1.2	2.9 \pm 1.4
Fledglings	4.1 \pm 1.7	3.1 \pm 1.1	2.9 \pm 1.2	2.6 \pm 1.3
Fledglings/eggs	75.0 \pm 9.2	65.8 \pm 21.3	66.3 \pm 18.5	64.9 \pm 25.1

boxes replicated the darkness found in deeper natural tree cavities by incorporating a baffle to shield the entrance hole from the nesting chamber and increase the protection of birds from weather and predators (Johnson 1990). Tree nest boxes were erected in areas lacking suitable buildings and were mounted on old tree stumps and telegraph poles 3 m above the ground. All boxes were lined with wood chips.

All sites were monitored at 8-wk intervals throughout the year. The frequency of visits was increased to every 3 wk during the breeding season from March to September at occupied sites. Egg clutch size and initial brood size

were determined at all sites. The number of young of fledging age was recorded during visits to band young at 5–6 wk of age.

Data were analyzed for differences in selection of site types and productivity between natural nesting sites and nesting boxes using Chi-square analysis. Because the data for the reproductive efforts were not normally distributed, data on clutch, brood, number of fledglings, and fledgling/egg among the four site types were compared using the Kruskal-Wallis test. Comparisons of clutch, brood, and fledglings/brood produced in natural sites and in all types of boxes were done using the Mann-Whitney *U*-test.

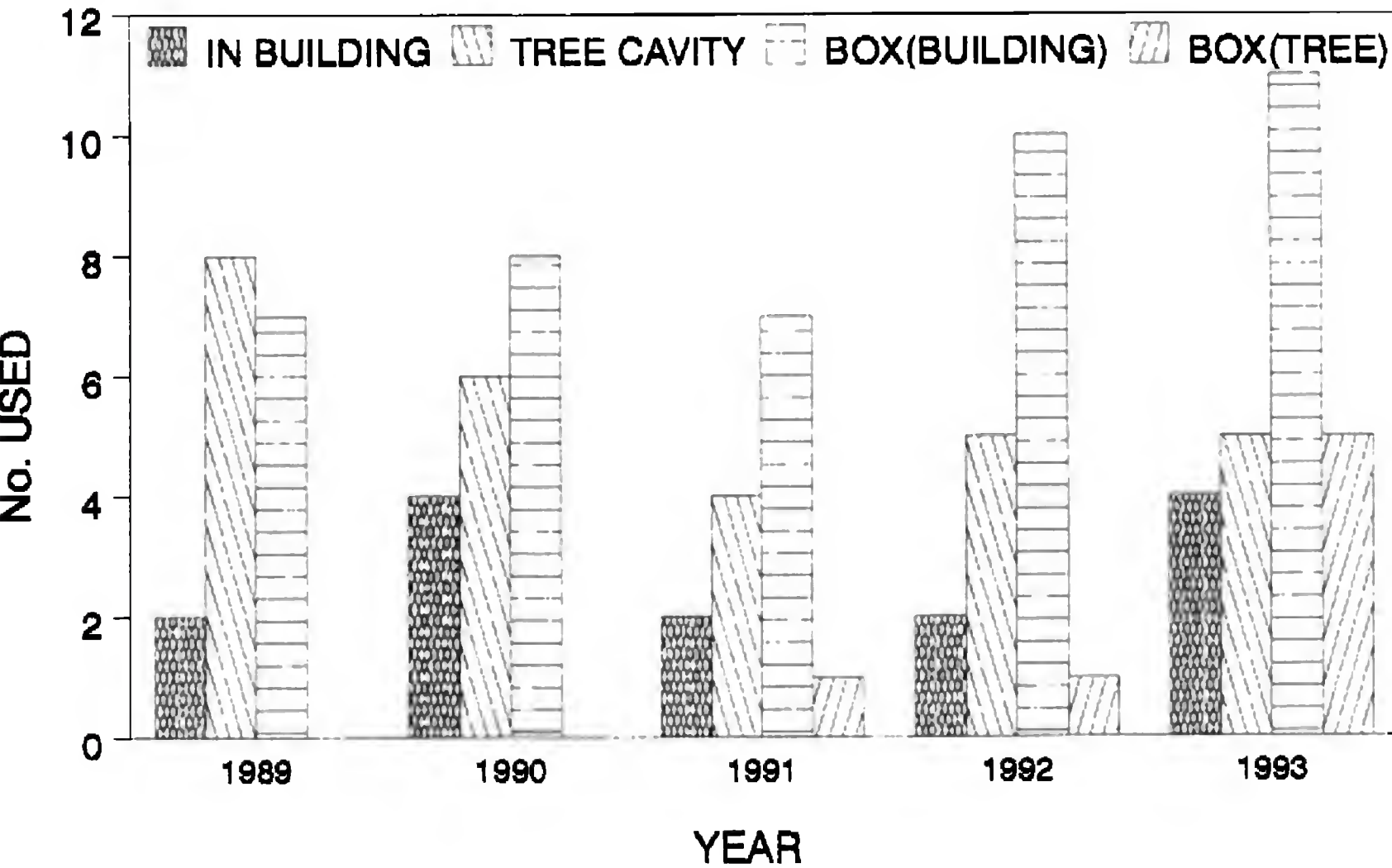


Figure 1. Nest sites available in the study area.

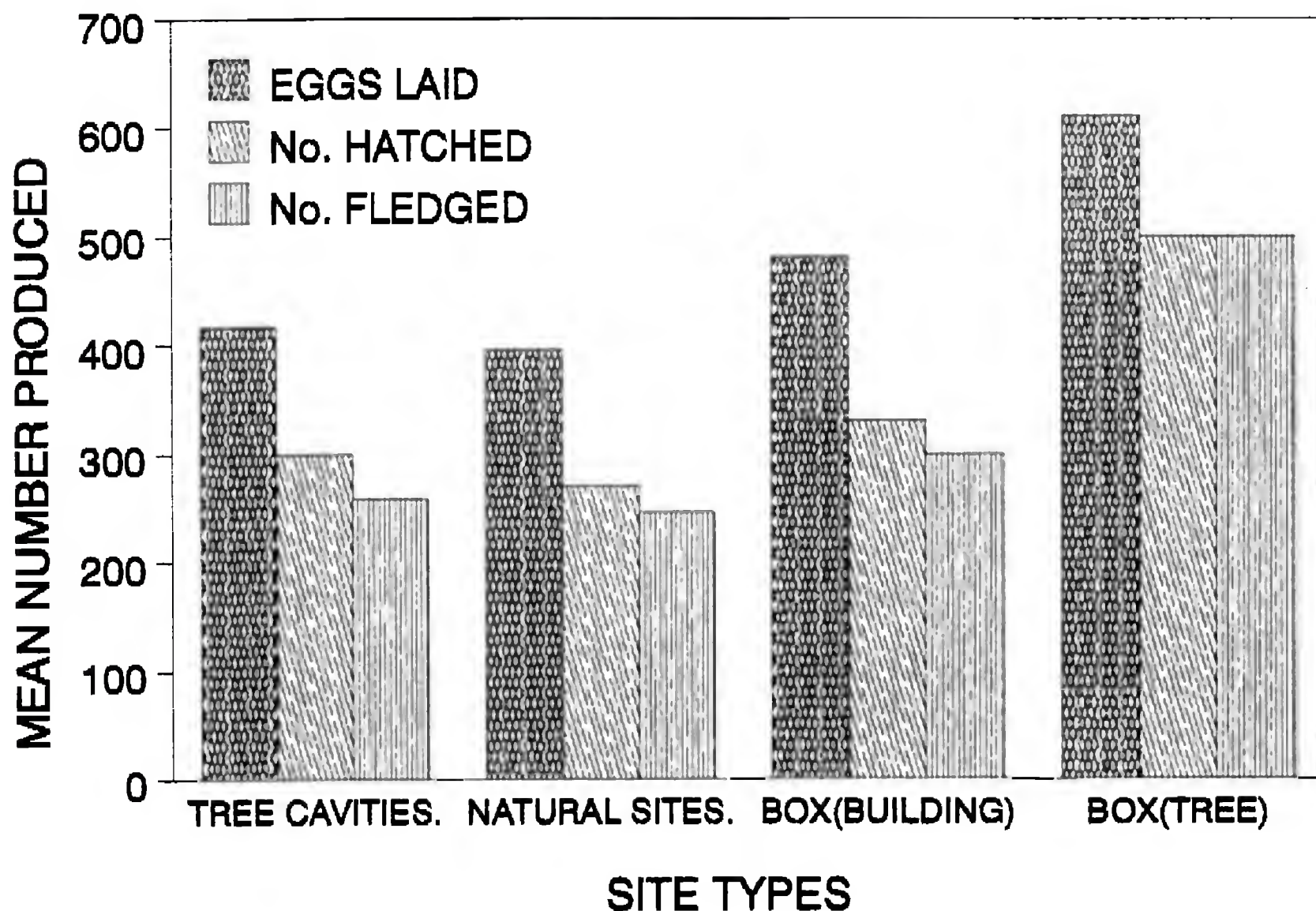


Figure 2. Nest site use by barn owls, 1989–93.

RESULTS AND DISCUSSION

Site use and reproductive data are shown in Table 1. Tree cavities were used at a higher rate than non-box sites in buildings ($P = 0.06$). The combined data for nest boxes versus all other types showed no significant difference in selection relative to availability ($\chi^2 = 0.3$, NS). Tree boxes produced more eggs, but not significantly more fledglings than other site types (Kruskal-Wallis, $H = 9.6$, $P = 0.02$ for clutch; $H = 6.3$, $P > 0.08$ for brood and fledglings).

Significant differences were found in the clutch and brood sizes and the numbers of young produced between nest boxes and other sites, but productivity of fledglings in relation to clutch sizes was comparable between natural and artificial sites, (Mann-Whitney $U = 802$, $P < 0.04$ for the first three, but $U = 1005$, NS for productivity). Therefore, box sites apparently do produce a greater reproductive effort, but not necessarily a greater reward. Overall, productivity of fledged young (number of young fledged/

number of eggs laid) in this study was 66.6% (SD = 20.3), which compares favorably with an average of 62.5% (SD = 14.8) for 11 other species of cavity-nesting owls (F.R. Gelbach pers. comm.).

My early survey results (Johnson 1991) showed a 58% use of large tree cavities and only 31% use of buildings by breeding owls in comparison to a national trend of 64.6% nesting in buildings and 24% in trees (Shawyer 1987). Within the study area, the three pairs nesting in buildings used lofts in derelict houses or abandoned military buildings. These findings are in line with other studies in the East Anglian region. Cayford (1992) also found a high proportion of nest sites in tree cavities; only buildings with lofts or nest boxes were used as breeding sites. Such features and natural sites were scarce in the area prior to this study (Fig. 1). Tree cavities were used in ash (*Fraxinus excelsior*; $N = 5$), oak (*Quercus robur*; $N = 5$), elm (*Ulmus procera*; $N = 3$), and beech (*Fagus sylvatica*; $N = 1$). The low annual rainfall in the region ($\bar{x} = 65$ cm compared to 100–300 cm nation-

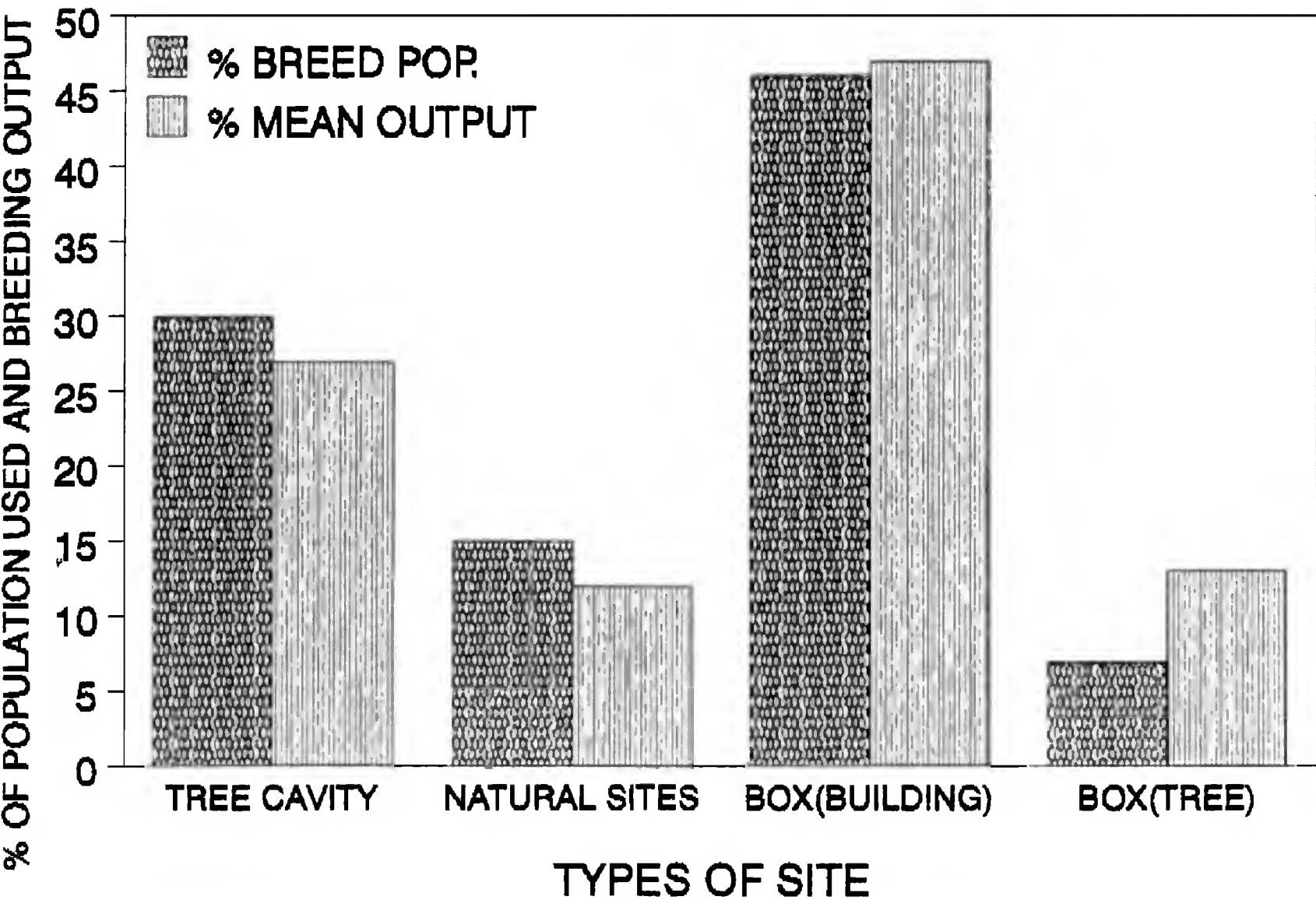


Figure 3. Reproductive performance by barn owls in four types of nest sites.

ally) is thought to be a critical factor allowing such open structures to be used successfully (Shawyer 1987). The loss of elms to disease across the region has significantly reduced the availability of tree cavities. Osbourne and Krebs (1981) estimated a loss of over 11 million trees nationally, which has increased competition among other cavity-nesting species.

The tawny owl (*Strix aluco*), often viewed as a nest-site competitor with the barn owl (Shawyer 1987), only used one box during this study. Whereas, the jackdaw (*Corvus monedula*) proved to be a major competitor for tree cavities and tree nest boxes requiring the annual removal of jackdaw nest material which would otherwise restrict access by barn owls.

Predation by a stoat (*Mustela erminea*) caused the permanent desertion of one nest box in a building, and deliberate human disturbance in buildings caused the loss of clutches during incubation.

The widespread felling of decaying trees has had

the greatest impact on the density of suitable natural breeding sites during this study. The observed trend for nesting barn owls was an increased use of nest boxes and a decline in the availability of natural tree cavities (Fig. 2). Eleven (25%) of the 43 nest boxes erected in buildings were used, together with five (41%) of the 17 tree boxes, increasing the breeding population density within the study area from 23 to 41 pairs, an increase of 178% during the 5 yr of the study. Much like the situation described by Lenton (1978), the increased barn owl population recorded in my study is attributable to the wider availability of good quality nest sites. Nesting sites were apparently a limiting factor on the population and without the provision of nest boxes the deterioration of natural sites available would have reduced the density of breeding pairs.

Data for all site types clearly show a reduction in brood size from the number of eggs laid (Fig. 3 and Table 1). This was attributable to the common oc-

currence of infertile eggs in clutches. A further reduction between hatching and fledging was recorded for all sites except tree boxes. Partial brood mortality is often a symptom of poor food supply to the brood (Southern 1959) but was attributable to predation in three present cases.

Taylor and Massheder (1992) using data from southwest Scotland, modeled a population that required a mean reproductive output of 3.2 young per pair to maintain a population and 3.5 young per pair to produce a sustained population growth. If applicable to this study area, only the pairs using nest boxes were achieving this level.

To safeguard this threatened species, nest boxes need to be correctly located and maintained in order to increase the potential breeding density determined by foraging area and prey density. For the mid- to long-term future in this area, conservationists must protect and enhance the remaining habitat and restrict tree felling across the region. A revival of historic tree management, particularly pollarding, would stimulate the growth of trees with widened trunk diameters and provide spacious natural cavities in time. Within this intensively human-manipulated environment, a comparison between "natural" and man-made structures is not valid. Many natural structures are in unnatural locations, only the quality of the structure and surrounding environment varies and perhaps directly influences the nesting success and density of the breeding barn owl population. Only species that build their own nests can locate in optimum foraging conditions. By selecting nest boxes in trees or buildings barn owls are adapting to an adequate substitute for losses of natural sites and show reproductive output equivalent to that of other sites.

ACKNOWLEDGMENTS

I would like to acknowledge the considerable support and assistance I have received from Fred Gehlbach in the analysis of my data and for his guidance in preparing this manuscript, and the support of Colin Shawyer throughout the years of field work. The Hawk and Owl Trust gratefully acknowledges the Goldsmiths Trust, the MacTaggart Third Fund and Hilleshog U.K. Ltd., for their support of this conservation project.

LITERATURE CITED

- BLAKER, G.B. 1933. The barn owl in England—results of the census. *Bird Notes News* 15:69–172; 207–211.
- BUNN, D.S., A.B. WARBURTON AND R.D.S. WILSON. 1982. The barn owl. T. and A.D. Poyser, Calton, U.K.
- CAYFORD, J. 1992. Barn owl ecology on East Anglian farmland. Royal Society for the Protection of Birds *Conservation Review* 6.
- JOHNSON, W.D. 1974. The bioenergetics of the barn owl (*Tyto alba*). M.S. thesis, California State Univ., Long Beach, CA U.S.A.
- JOHNSON, P.N. 1990. Experimenting with nestboxes, Norfolk barn owl boxes. *Br. Trust Ornithol. News* No. 169:5.
- . 1991. Barn owls in North Norfolk. *Norfolk Bird Mammal Rep.* 1990:91–95.
- KORPIMÄKI, E. AND S. SULKAVA. 1987. Diet and breeding performance of Ural owls under fluctuating food conditions. *Ornis Fenn.* 64:57–66.
- LENTON, G.M. 1978. Owls as rat controllers—a preliminary report. *Planter, Kuala Lumpur* 54:72–83.
- MØLLER, A.P. 1989. Parasites, predators and nest boxes facts and artefacts in nest box studies of birds? *Oikos* 56:421–423.
- . 1992. Nest boxes and the scientific rigour of experimental studies. *Oikos* 63:309–311.
- OSBOURNE, L. AND J. KREBS. 1981. Replanting after Dutch elm disease. *New Scientist* 90:212–215.
- SAUROLA, P. 1989. Breeding strategy of the Ural owl (*Strix uralensis*). Pages 235–240 in B.-U. Meyburg and R.D. Chancellor [EDS.], *Raptors in the modern world*, World Working Group on Birds of Prey and Owls Berlin, Germany.
- SHAWYER, C.J. 1987. The barn owl in the British Isles, its past, present and future. *Hawk Trust*, London, U.K.
- SOUTHERN, H.N. 1959. Population ecology, mortality and population control. *Ibis* 101:429–436.
- . 1970. The natural control of a population of tawny owls (*Strix aluco*). *J. Zool. (Lond.)* 162:197–285.
- TAYLOR, I.R. AND J. MASSHEDER. 1992. The dynamics of depleted and introduced farmland barn owl (*Tyto alba*) populations, a modelling approach. Pages 105–110 in C.A. Galbraith, I.R. Taylor and S. Percival [EDS.], *The ecology and conservation of European owls*. Joint Nature Conservation Committee, Peterborough, U.K.

Received 3 December 1993; accepted 25 May 1994

NEST-BOX VERSUS NATURAL-CAVITY NESTS OF THE EASTERN SCREECH-OWL: AN EXPLORATORY STUDY

FREDERICK R. GEHLBACH

Department of Biology, Baylor University, Waco, TX 76798 U.S.A.

ABSTRACT.—The use of nest boxes versus natural tree cavities by eastern screech-owls (*Otus asio*) in central Texas was explored for 9 yr. Box sites resembled natural-cavity sites vegetatively and physically except that the boxes were positioned somewhat lower. The three box sizes provided spanned the size range of natural cavities used by screech-owls. Box size made no difference in nest site selection, clutch size, or nesting success. Three kinds of wood used in box construction made no difference either. The largest boxes were used more often for replacement nests, and the smallest ones tended to crowd broods, contributing slightly to mortality and early fledging. Overall, nest boxes produced data on frequency of use, clutch size, and fledgling productivity that were equivalent to data from natural cavities.

KEY WORDS: *breeding success; eastern screech-owl; nest boxes; nest-site use; Otus asio; tree-cavity nests.*

Nidos en cajas anideras versus cavidades naturales de *Otus asio*: un estudio exploratorio

RESUMEN.—Se exploró por nueve años el uso de cajas anideras versus cavidades naturales ubicadas en árboles por parte de *Otus asio* en el centro de Texas. Las cajas anideras se asemejaron a las cavidades naturales tanto vegetativa como físicamente, excepto que las cajas fueron ubicadas algo más abajo. El tamaño de las cajas utilizadas correspondía al espectro de tamaños de las cavidades naturales usadas por *O. asio*; no se registraron diferencias en la selección de sitio de nidificación, tamaño de la nidada o éxito de los polluelos. Tres tipos de maderas se utilizaron en la construcción de las cajas y tampoco se registraron diferencias. Las cajas más grandes fueron utilizadas a menudo para reemplazo de nidos y en las más pequeñas se tendía a agrupar las crías, aumentando ligeramente la mortalidad y un desarrollo precoz. En general, las cajas anideras producen datos sobre la frecuencia de uso, tamaño de nidada y productividad de volantones que fueron equivalentes a los obtenidos desde cavidades naturales.

[Traducción de Ivan Lazo]

Many raptor researchers employing artificial structures like nest boxes or nesting platforms do not utilize or report simultaneous comparisons with natural structures or distinguish site suitability or availability in studying habitat selection. Møller (1989, 1992) and Clobert and Lebreton (1991) note possible deficiencies in such studies using nest boxes, including the potential for greater nesting success in boxes than natural cavities. Here, I focus on the simultaneous comparison of eastern screech-owls (*Otus asio*) nesting in boxes and natural tree cavities to discover if there was a difference in the use of and breeding success in the two site types.

Field studies of birds may need to be conducted over several years during which investigative biases can multiply errors. Consequently, I tested for biases that might result from using nest boxes prior to conducting a 16-yr population study of the eastern screech-owl (Gehlbach 1994). Among cavity-nesting

owls, only the boreal or Tengmalm's owl (*Aegolius funereus*) has been studied in a somewhat similar manner; clutch size and number of fledglings of that species were determined in both nest boxes and natural cavities but not in controlled fashion (Korpi-mäki 1984).

METHODS

The study was conducted in 135 ha of Woodway, a suburb of Waco, TX, U.S.A., during 1967–75. This area had 508 human residents/km² and 25.9% green space averaging 327–1504 trees/ha in lawns and wooded ravines, respectively. Eastern screech-owls and the natural tree cavities they used were located by mapping cavity-advertisement songs and making cavity inspections in December through early March before nesting began. I continued to search for used and unused but apparently suitable cavities (as large or larger than used cavities; McCallum and Gehlbach [1988]) until the cumulative number found versus cumulative search effort indicated that essentially all were known.

Nine nest boxes were constructed, three each of exterior

plywood, solid pine, and solid cedar (1.9-cm-thick wood), and were painted dark brown on the outside. Cavity size has been shown to influence clutch size in owls (Korpimäki 1985), and to test its affect on screech-owls I built one box of each wood type with 225, 400, and 625 cm² bottoms. All boxes had a 6.8 cm entrance hole 25 cm above the box bottom. The bottom areas of these boxes spanned those of natural cavities. Depth of the boxes was the average of 12–58-cm-deep natural cavities, and the entrance diameter was the mean minimum dimension of the natural entrances.

Box locations depended on landowner permission and were placed 70–300 m from natural cavities used by screech-owls and other boxes on straight tree trunks. Trunk diameters at these positions were equal to or larger than box width. Boxes faced nine different directions and were 3–4 m above ground. Five boxes were paired with the closest previously used natural cavities most like them in orientation, height, and volume. The other four could not be paired because it required several years to discover all natural sites used by screech-owls. I evaluated only first-nest data, since replacement nests are so different (Gehlbach 1994).

A 75-m, 5-point, 20-quarter transect, randomly aligned through each box and cavity tree, was employed to assess vegetational features according to Gehlbach (1988, 1994). These and physical measurements were made before the boxes were positioned, so that box sites would resemble natural cavity sites. Measurements and syntheses concerned tree and shrub density, height, and diversity, the evergreen fraction, canopy coverage, tree species relative importance, nest tree diameter, nest height and bottom area, and distance to the nearest house, permanent water, and suitable/available cavity or box.

Several handfuls of dried leaves were placed in the bottom of each box to simulate an old fox squirrel (*Sciurus niger*) nest because all but one of the used natural cavities had them. Thereafter, box and cavity contents were undisturbed except in a minor way during nest inspections. Fox squirrels and other cavity users and nest predators were not disturbed during the weekly surveys of nest contents which extended through June, and nest debris was not removed between years.

Multifactor box versus natural-cavity environments, high- versus low-use boxes, and used versus unused natural cavities were evaluated with multivariate analyses employing transformed data. Individual parameters were then tested with univariate analysis of variance. Use and reproductive data for the box/cavity pairs were assessed with Wilcoxon signed-ranks tests, while unpaired data were subjected to Mann-Whitney *U*-tests. Spearman rank correlations were used to test relationships between box size and nest contents. Chi-square analyses were made of nests in boxes versus cavities, use of and results from the different box sizes and wood types, and box versus cavity dispersions among dominant trees.

Means, standard deviations, sample sizes (if not obvious from the designs), and exact probabilities are given except for those >0.10, which I consider non-significant (NS) in two-tailed tests. Probabilities of <0.10 have potential biological meaning in view of my confirmatory study (Gehlbach 1994).

RESULTS

Nest Cavities and Habitat. Of the 23 suitable natural cavities that I found, eastern screech-owls nested in 15 that were deeper (>25 cm) with larger floors (>10 cm minimum dimension) and had smaller entrances (<15 cm maximum dimension) than the others (MANOVA $F = 2.9$, $P = 0.04$). The used sites were 3.7 m (SD = 1.6) above ground in naturally rotted, hollow limbs or tree trunks. At least 10 of these cavities had been enlarged by fox squirrels. The red-bellied woodpecker (*Melanerpes carolinus*), the largest local woodpecker species, did not excavate cavities large enough for screech-owls.

Paired box- and natural-cavity sites were 72–280 m apart and similar in their vegetational and physical features (MANOVA $F = 1.1$, NS). However, the boxes tended to be lower ($\bar{x} = 3.1$ vs. 3.7 m, ANOVA $F = 3.5$, $P = 0.06$) and in smaller diameter trees ($\bar{x} = 26.7$ vs. 32.2 cm, $F = 2.4$, $P = 0.09$). While all nine nest boxes were placed lower in smaller trees than the 15 used natural cavities (ANOVA $F = 3.2$, $P < 0.05$), both site-types were equally distributed among the seven most common trees of the canopy ($\chi^2 = 1.7$, NS). Cedar elm (*Ulmus crassifolia*) was the dominant tree and had the most natural cavities (48%) and boxes (44%).

The frequencies with which screech-owls used paired boxes and natural cavities for nesting were quite similar, and similar to all nine boxes and nine cavities with at least 5-yr records (Table 1). Type of wood and box size made no difference in nest box selection; useage relative to availability ranged from 60% in pine and 67% in small boxes to 70% in cedar and 73% in large boxes ($\chi^2 = 1.7$, NS).

Preferred nesting habitat was distinguished as having more evergreens in the canopy, lower tree density, closer alternate nest site, and lower shrub density in first-to-last order of importance ($F = 4.0$, $P < 0.07$). This combination of features describes a shady, park-like landscape with large, cavity-prone trees at low densities. These habitat characteristics were identified by subjecting 12 high- and 12 low-use nest sites (employing the 60% median use rate of all nine boxes plus 15 cavities) to stepwise discriminant analysis.

Reproduction. Clutch size and number of fledglings/clutch in the nest boxes were statistically like those in natural cavities (Table 1). Clutch size in the 29 nests in boxes were not related to bottom area of the box ($r_s = 0.17$, NS) unlike the situation in

Table 1. Eastern screech-owl use of and breeding success in nest boxes and natural cavities, 1967–75. Means \pm standard deviations and sample sizes (in parentheses) are of first nests only.^a

PARAMETERS	NEST BOXES	NATURAL
CAVITIES		
Site use (%)		
Pairs ^b	64.2 \pm 13.0 (5)	75.8 \pm 19.1 (5)
All ^b	70.5 \pm 15.3 (9)	77.5 \pm 16.2 (9)
Successful nests (%) ^c		
Pairs ^b	67.8 \pm 21.2 (5)	81.1 \pm 12.4 (5)
All ^b	70.7 \pm 18.6 (9)	72.8 \pm 15.7 (9)
Clutch size	3.9 \pm 0.5 (29)	3.8 \pm 0.6 (16)
Fledglings/eggs (%)	51.3 \pm 16.8 (29)	57.0 \pm 19.4 (16)

^a Wilcoxon $Z < 0.9$, NS, for all paired data comparisons; Mann-Whitney $U < 19$, NS, for all unpaired data comparisons.
^b Pairs = five boxes each paired with a natural tree cavity having similar environmental features; all = the paired boxes and cavities plus four more boxes and four cavities with at least 5-yr records.
^c At least one chick fledged.

boreal owls (Korpimäki 1985). But when chick losses occurred, they were 21% higher in the smallest boxes versus larger ones and slightly more frequent there (31% vs. 20%; $\chi^2 = 1.7$, NS). Also, chicks fledged somewhat sooner from smaller boxes ($r_s = 0.39$, $P = 0.06$). Successful nests tended to be more frequent in paired natural cavities but not significantly so, and the larger samples of nine sites each were essentially alike (Table 1).

Possible Inspection Biases. Screech-owls used only 65.6% (SD = 18.6) of the available paired boxes and tree cavities in 1968–71 compared to 78.1% (SD = 20.9) in the following 4 yr (Wilcoxon $Z = 2.0$, $P = 0.04$). Demand for nesting space was apparently not a factor because the mean use of 20 suburban boxes was not significantly different over the next 16 yr despite a nearly two-fold flux in population density ($\bar{x} = 75.6\%$, SD = 16.1; Mann-Whitney $U = 11$, NS; Gehlbach 1994). Moreover, productivity in the paired boxes plus cavities was only 45.9% (SD = 39.3) in 1968–71 but rose to 55.6% (SD = 40.7) in 1972–75 (Wilcoxon $Z = 1.4$, NS) and remained about the same in the following 16 yr (53.8%, SD = 15.6; Mann-Whitney $U = 19$, NS).

DISCUSSION

Clearly, nest boxes are essentially equivalent to natural tree cavities and hence are a legitimate tool

in the study of eastern screech-owls. By contrast, Korpimäki (1984) found more eggs and fledglings of boreal owls in boxes than natural cavities, although he did not study both site-types concurrently. Southern (1970 and pers. comm.) made same-season comparisons of cavity- and box-use by tawny owls (*Strix aluco*), but did not enumerate cavity-nest contents. He found that 33–75% of the owls used boxes annually. Most students of cavity-nesting raptors assume that nest boxes provide natural data, even though Korpimäki (1984) suggests otherwise (also see Gauthier 1988, Robertson and Rendell 1990).

The overall 67% use rate of boxes in my study is considerably higher than 4–13% values reported for eastern screech-owls by Van Camp and Henny (1975), McComb and Noble (1981), and Fowler and Dimmick (1983). Perhaps this is because I placed boxes in sites similar to natural cavities after making environmental measurements. The high use was not due to an unusually dense or protected suburban population, or to a scarcity of suitable natural cavities which outnumbered the boxes. In fact, a much sparser rural population with twice as many natural nest sites per breeding pair of owls had box-use rates averaging 61% concurrently with a 70% use in suburbia (Gehlbach 1994).

Nest boxes closely matching used natural cavities furnish vital information on nest-site selection and the influence of cavity size on chick mortality and fledging. Korpimäki (1984, 1985) obtained results different from mine using different size boxes but his study did not attempt to differentiate among the variety of available natural sites. When boxes are used to compensate for the scarcity of natural tree cavities to manage owl populations (e.g., Saurola 1989), I suggest that one simulate the range of natural nest cavities, since cavity size can influence some aspects of reproduction.

Comparing environmental features used by a species versus randomly selected environmental features is incorrectly called habitat selection (e.g., Cody 1985). Habitat that is suitable for a species must be distinguished from all available habitat. In fact, some randomly chosen sites may be unsuitable, and raptors may not use all possible sites unless forced to by population pressure. Studies of habitat selection must include environments that have been and could be used besides those now used, and thus furnish a spectrum of conditions for selection by birds under various population densities. Measurements are based on criteria like the mean-minimum dimensions of

past and current use (McCallum and Gehlbach 1988).

Although the nest-box method proved to be valid for studying eastern screech-owls, I believe boxes attracted deleterious human attention early in my study when they were novel. In addition, my own learning of inspection techniques may have inadvertently focused on the lower and hence readily accessed boxes despite attempts to treat all paired sites equally. This could have produced the disparate early- versus late-study results, because frequency of site use and productivity did not change appreciably during population flux over the next 16 yr. Thus, I advise that population investigations be preceded by explorations that refine all investigative approaches, not just the use of substitute habitats.

ACKNOWLEDGMENTS

I thank the many persons mentioned in Gehlbach (1994), especially George Newman and Claudia and the late C.W. Davis, whose nest boxes I watched before designing this study. Jeffrey Marks and anonymous reviewers provided constructive comments on the manuscript.

LITERATURE CITED

- CLOBERT, J. AND J.D. LEBRETON. 1991. Estimation of demographic parameters in bird populations. Pages 75-104 in C.M. Perrins, J.D. Lebreton, and G.J.M. Hirons [EDS.], *Bird population studies: relevance to conservation and management*. Oxford Univ. Press, New York, NY U.S.A.
- CODY, M.L. [ED.]. 1985. *Habitat selection in birds*. Academic Press, New York, NY U.S.A.
- FOWLER, L.J. AND R.D. DIMMICK. 1983. Wildlife use of nest boxes in eastern Tennessee. *Wildl. Soc. Bull.* 11: 178-181.
- GAUTHIER, G. 1988. Factors affecting nest-box use by buffleheads and other cavity-nesting birds. *Wildl. Soc. Bull.* 16:132-141.
- GEHLBACH, F.R. 1988. Forests and woodlands of the northeastern Balcones Escarpment. Pages 57-77 in B.B. Amos and F.R. Gehlbach [EDS.], *Edwards plateau vegetation: plant ecological studies in central Texas*. Baylor Univ. Press, Waco, TX U.S.A.
- . 1994. *The eastern screech owl: life history, ecology, and behavior in the suburbs and countryside*. Texas A. and M. Univ. Press, College Station, TX U.S.A.
- KORPIMÄKI, E. 1984. Clutch size and breeding success of Tengmalm's owl *Aegolius funereus* in natural cavities and nest boxes. *Ornis Fenn.* 61:80-83.
- . 1985. Clutch size and breeding success in relation to nest-box size in Tengmalm's owl *Aegolius funereus*. *Holarctic Ecol.* 8:175-180.
- MCCALLUM, D.A. AND F.R. GEHLBACH. 1988. Nest-site preferences of flammulated owls in western New Mexico. *Condor* 90:653-661.
- MCCOMB, W.C. AND R.E. NOBLE. 1981. Nest-box and natural cavity use in three midsouth forest habitats. *J. Wildl. Manage.* 45:93-101.
- MØLLER, A.P. 1989. Parasites, predators and nest boxes facts and artefacts in nest box studies of birds? *Oikos* 56:421-423.
- . 1992. Nest boxes and the scientific rigour of experimental studies. *Oikos* 63:309-311.
- ROBERTSON, R.J. AND W.B. RENDELL. 1990. A comparison of the breeding ecology of a secondary cavity-nesting bird, the tree swallow (*Tachycineta bicolor*) in nestboxes and natural cavities. *Can. J. Zool.* 68:1046-1052.
- SAUROLA, P. 1989. Breeding strategy of the Ural owl, *Strix uralensis*. Pages 235-240 in B.-U. Meyburg and R.D. Chancellor [EDS.], *Raptors in the modern world*. World Working Group on Birds of Prey. Berlin, Germany.
- SOUTHERN, H.N. 1970. The natural control of a population of tawny owls (*Strix aluco*). *J. Zool. (Lond.)*. 162:197-285.
- VAN CAMP, L.F. AND C.J. HENNY. 1975. *The screech owl: its life history and population ecology in northern Ohio*. U.S. Fish and Wildl. Serv. N. Am. Fauna No. 71.

Received 3 December 1993; accepted 18 July 1994

THE POST-FLEDGING DEPENDENCE PERIOD OF THE LESSER KESTREL (*Falco naumanni*) IN SOUTHWESTERN SPAIN

JAVIER BUSTAMANTE AND JUAN JOSÉ NEGRO¹

Estación Biológica de Doñana, CSIC, Pabellón del Perú, Avda. María Luisa s/n, 41013-Sevilla, Spain

ABSTRACT.—We studied the post-fledging dependence period of individually marked lesser kestrels (*Falco naumanni*) in southwestern Spain. Chicks fledged at a mean age of 37 d and remained at the breeding colony, depending on their parents for food, on average 5 d more. Parents declined food provisioning to offspring during the post-fledging dependence period. We did not observe play with objects, social play, training or learning of hunting skills among the fledglings. Family groups dissolved once the fledglings dispersed from the colony. The adults tend to remain at the breeding colony while juveniles have been observed up to 164 km NE-NW from their natal colony before starting fall migration.

KEY WORDS: *dispersal; Falco naumanni; fledging; lesser kestrel; post-fledging.*

El periodo de emancipación del Cernícalo Primilla (*Falco naumanni*) en el suroeste de España

RESUMEN.—Estudiamos el período de emancipación de Cernícalos Primilla (*Falco naumanni*) marcados individualmente en el suroeste de España. Los pollos realizaron sus primeros vuelos a una edad media de 37 días y permanecieron en la colonia de cría, dependiendo de las presas aportadas por sus padres, una media de 5 días más. Los padres fueron disminuyendo la cantidad de presas aportadas a su descendencia durante el periodo de emancipación. No observamos que los jóvenes cernícalos jugaran con objetos, realizaran persecuciones u otros juegos sociales ni aprendieran o practicasen la captura de presas antes de emanciparse. Los grupos familiares se disolvieron una vez que los jóvenes abandonaron la colonia de cría. Los adultos tienden a permanecer en la colonia de cría mientras que algunos jóvenes han sido observados hasta a 164 km de su colonia natal en dirección NE-NO antes de iniciar la migración postnupcial.

[Traducción Autores]

The period from fledging to independence is known as the post-fledging dependence period and very little is known about this period for most species of raptors. No published information on the length of this period exists for the lesser kestrel (*Falco naumanni*). Brown and Amadon (1968) said that chicks fledge 26–28 d after hatching and are fed at the nest and in the vicinity of the colony for some time after that, apparently based on a few observations made by Blondel (1964) on two nests in the south of France. According to Pomarol (1990), chicks hatched in captivity and released by hacking, although able to fly at 30 d of age, delayed their first flight till 35–40 d old, and remained 0–25 d at the hacking site before dispersing.

In this study we report the first detailed data on fledging age, duration of the post-fledging dependence period, and behavior during this period of individually marked lesser kestrels in the wild.

STUDY AREA AND METHODS

The post-fledging dependence period of lesser kestrels was studied during 1989 at a breeding colony in the castle of Mairena del Alcor (37°22'N, 5°45'W), Seville, southwestern Spain. The study area is an agricultural plain in the Guadalquivir River basin with small fields of cereals (wheat and barley), sunflowers, olive and fruit trees. The colony consisted of 42 pairs of lesser kestrels breeding in holes in the walls of the castle.

Five neighboring nests (brood-sizes: 4, 4, 3, 2 and 2 chicks), referred hereafter as focal nests, were selected for observations during late nestling and post-fledging dependence period, but only three of these nests produced fledglings. All focal nests could be observed simultaneously from a point 70 m from the colony. All the adults attending the focal nests, except one male and one female, had been banded with laminated plastic bands with an alphanumeric code. The adult male and female attending one of the focal nests were also equipped with a radiotransmitter

¹ Present address: Avian Science and Conservation Centre, Macdonald Campus of McGill University, 21,111 Lakeshore Road, Ste. Anne de Bellevue, Quebec H9X 3V9, Canada.

Table 1. Lesser kestrels banded as nestlings and recovered or resighted in a locality different from their natal locality before fall migration.

BANDING LOCALITY	BANDING DATE	RECOVERY LOCALITY	RECOVERY DATE	Dis-TANCE TRAV-ELED (km)	DIRECTION TRAVELED	AGE AT RECAP-TURE ^a
Arahal	23 June 1988	Fuencaliente	14 July 1988	164	NNE	31 d
Arahal	23 June 1989	Lora del Río	22 July 1989	44	N	49 d
Morón	29 June 1989	Arahal	17 July 1989	18	NNW	34 d
Arahal	10 July 1989	Hinojos	25 August 1989	75	W	78 d
Mairena	5 July 1991	Hacienda Ntra. Sra. de la Luz	18 August 1991	3	E	40 d
Arahal	3 July 1991	Mairena	10 September 1991	22	NW	89 d

^a Days after hatching.

(5 g, 3% of body mass) attached to two central tail feathers (Kenward 1978).

All nestlings in the colony ($N = 59$) were banded with laminated plastic bands and 10 (including one from a focal nest) were also equipped with a radiotransmitter (5 g) attached with a back-pack harness (Beske 1978). Observations of the post-fledging period at the colony started the 7 July before the first chick of a focal nest fledged and ended the 25 July when all the fledglings from focal nests had abandoned the colony. We performed 4-hr observation periods every 1–2 d, at different times of the day from sunrise to sunset, totalling 36 hr of observations at the colony. One observer (J.B.) remained at the colony while two observers in a vehicle simultaneously tracked the adults equipped with radiotransmitters or tried to locate the fledglings that were dispersing.

At least every 2 d we checked at sunset to find if individuals equipped with radiotransmitters were roosting at the colony. When fledglings started to disperse, we included other roosts habitually used by adults in a 4 km radius of the colony in our sunset checks. We performed checks until all fledglings with radiotransmitters had disappeared from the neighborhood of the colony (31 July).

Hatching date was known for some chicks and for the remaining individuals it was estimated from the length of the 8th primary feather at the time of banding (Donazar et al. 1991). Because hatching asynchrony is small (J.J. Negro unpubl. data) a mean hatching date—obtained from the estimates for each sibling—was assigned to each brood. Fledging date was the first date a chick was observed flying or on a perch it could not have reached walking from the nest. We considered that focal fledglings no longer being fed by their parents at the colony were independent, and that fledglings with radiotransmitters no longer roosting at the colony at sunset had dispersed.

Since 1988, chicks at the colony of Mairena and at two other colonies in a 40-km radius (Morón and Arahal), have been marked with plastic bands. From 1988 to 1992, during the period from fledging to fall migration (July and August), the colonies were visited regularly for other studies. The identity and location of chicks present at the

colony was recorded and their age was estimated from the length of the 8th primary feather at banding. Observations were classified in two categories: (1) chicks at the entrance of their nest or on a perch they could have reached walking from it, and (2) chicks seen flying or on a perch they could only have reached by flying. To check if chicks observed in 1989 in Mairena fledged at an older age than is typical for this area, we compared the distribution of observations of chicks of different ages considered to be flying from Mairena in 1989 ($N = 38$) with that from Mairena, Morón and Arahal in 1988, 1990, 1991 and 1992 ($N = 100$) with a Kolmogorov-Smirnov two-sample one-tailed test (Siegel and Castellan 1988).

RESULTS

Fledging Age and Duration of the Post-fledging Dependence Period. Chicks from the focal nests fledged at a mean age of 37.1 d (range 36–40 d, $SD = 1.6$, $N = 7$). Fledglings from the focal nests became independent a mean of 5.1 d after fledging (range 2–8 d, $SD = 1.9$, $N = 7$), at a mean age of 42.4 d (range 39–40 d, $SD = 1.7$, $N = 7$). Fledglings with radiotransmitters dispersed at a mean age of 42 d (range 36–46 d, $SD = 3.1$, $N = 7$). The only focal fledgling with radiotransmitter became independent and dispersed on the same day at an age of 42 d.

Kestrels in 1989 were not seen flying at the colony at significantly older ages than in the years 1988, 1990, 1991, and 1992 pooled (Kolmogorov-Smirnov test $D_{38, 100} = 0.097$, $\chi^2 = 1.036$, $df = 2$, $P > 0.5$). No chick younger than 32 d was recorded at a colony as able to fly (Fig. 1), although a chick was recovered 31 d after hatching 164 km from its natal colony (Table 1). There are few observations of chicks older than 42 d still present at their natal colony (Fig. 1).

Fledgling Behavior. Fledglings remained close

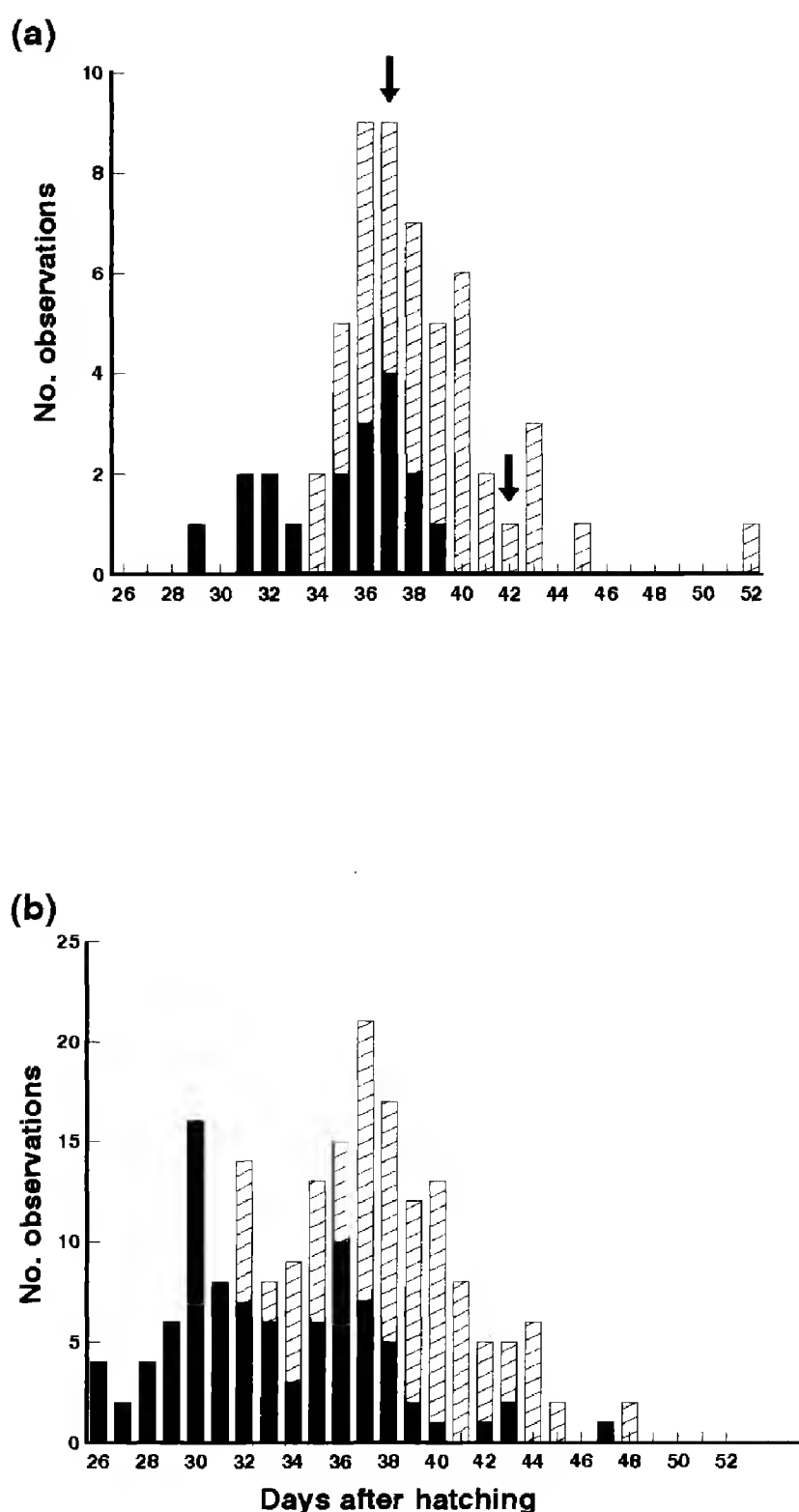


Figure 1. Frequency distribution of observations at breeding colonies of juveniles of known age around the time of fledging classified as still in their nest (solid bar) or able to fly (striped bar). (a) Data from Mairena 1989. The arrows show the average fledging age and average dispersal age of focal fledglings. (b) Data from Mairena, Morón and Arahal 1988, 1990, 1991 and 1992.

to their nests during the post-fledging dependence period, and most of the perching sites used were within 100 m of the nest. They made short flights between perches, wandered around the colony, and frequently entered other kestrels' nests. Fledglings never showed any signs of aggression toward other lesser kestrels—adults or chicks—that came close to

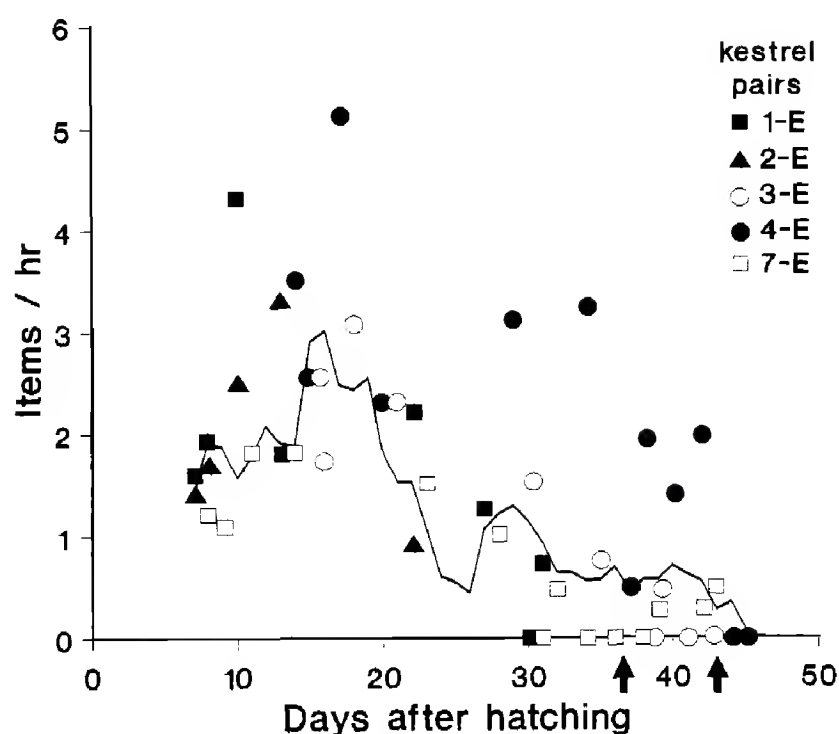


Figure 2. Feeding frequency during the nestling and post-fledging periods at the five lesser kestrel focal nests, estimated from 4-hr observation periods. The line is a moving average smoothing of the data with a 5-d span. The arrows show the average fledging age and the average dispersal age of the fledglings. At nests 1-E and 2-E all chicks died before fledging.

them or that eventually entered the fledgling's nest. Fledglings were observed on 30 occasions begging to kestrels that were not their parents (22 occasions begging to adults and 8 to fledglings). We did not observe fledglings catching prey, playing with objects, or chasing other kestrels or other birds (121 hr \times fledgling).

Adult Behavior. Both parents continued to feed their offspring during the post-fledging dependence period. Adults fed their fledglings at the colony with big- and medium-sized invertebrates (mainly Orthoptera) that they brought in their bills. Parents initially flew with prey to their nest but when their offspring were not there, they searched around the colony. Observed prey transfers took place at the nest (50% of all prey transfers, $N = 25$) or at perches within 100 m of it. No aerial prey transfers were observed. Daily feeding frequency during fledging and post-fledging periods (3.3 items/juvenile, $SD = 1.3$, $N = 3$ pairs) was lower than during the nestling period (10.3 items/juvenile, $SD = 3.2$, $N = 5$ pairs), and tended to decrease through the post-fledging dependence period (Fig. 2).

The breeding pair equipped with radiotransmitters decreased not only the number of prey they

brought but the number of visits they made to the colony throughout the post-fledging dependence period, and stopped feeding their offspring before the fledglings left the colony. These two adults were radiotracked for 12 hr, on three different days, during the post-fledging dependence period and for 15 hr on days two and four after their offspring dispersed. Neither the male nor the female was observed with any of its offspring away from the colony. These adults continued roosting near the colony the 31 July after all the fledglings with radiotransmitters had dispersed.

Breeding adults behaved aggressively toward lesser kestrels that were not their offspring that perched close to or came into their nest. We observed 22 aggressive interactions by kestrels and always the aggressor was an adult. In the 18 instances that the identity of the aggressor was known, it was an adult attending a nest within 2 m. At least 55% of the aggressive acts were directed toward unrelated fledglings and 32% toward adults. In three instances an adult kestrel evicted a fledgling from a different nest that had entered the adult's nest. However, in one instance an adult, after initially trying to avoid it, fed a fledgling from a different nest that had entered the adult's nest.

Fledgling Mortality. Eighteen of 25 chicks (51%) from the focal nests or other neighboring nests, plus the nine other chicks marked with radiotransmitters, died at around the time of fledging. The chicks were found dead at ages between 17–35 d (mean age at death 27.8 d, SD = 4.3, $N = 14$) and all seemed to have died from starvation (Negro et al. 1993b).

Fledgling Dispersal. Lesser kestrel migration at Gibraltar Straits peaks around the 15 September (Bernis 1980). All lesser kestrels banded as nestlings during 1988–91 and observed or recovered in July and August of the same year away from their natal colony had moved 3–164 km in directions north, east, and west (Table 1).

DISCUSSION

The mean fledging age of 37 d that we observed was 32% higher than the 26–28 d estimate quoted by other authors (Brown and Amadon 1968, Newton 1979, Cramp and Simmons 1980), but agrees with the observations of Pomarol (1990) on birds released by hacking. Lesser kestrels' reproductive success was poor in 1989, as was shown by the high mortality from starvation around the time of fledging (50% mortality). The growth of the surviving chicks may

also have been retarded thus delaying the fledging age, as seems to happen in other raptors feeding on prey with unpredictable abundance (Viñuela and Bustamante 1992). However, the ages at which chicks were observed out of the nest in other years and colonies (Fig. 1a) still suggests that lesser kestrels in southwestern Spain fledged on average at an older age than the estimate given in general sources (Brown and Amadon 1968, Newton 1979, Cramp and Simmons 1980). The 26–28 d period estimate was a rough estimate made by Blondel (1964) who observed only two nests.

The post-fledging dependence period observed was very short compared to that of other raptors. Low food availability in the area might have had an effect on this, although, in general, when food availability is low raptors tend to have longer post-fledging dependence periods (J. Bustamante unpubl. data). We think that juveniles became independent once they left the colony because the two adults radiotracked never interacted with their offspring away from the colony, and did not leave the neighborhood of the colony when their offspring did. None of the fledglings with radiotransmitters could be found after dispersal at the roosts habitually used by breeding adults in a 4-km radius of the colony (Negro et al. 1993a), and were not found in a 10-km radius of the colony while we were tracking the adults with radiotransmitters. Adults did not hunt far from the colony. The largest distance from the colony traveled by radiotracked adults during the nestling period was 14.5 km for females and 8 km for males (Negro et al. 1993a).

Lesser kestrel migration peaks in September, 45 d after all the fledglings of our colony had dispersed. Observations and recoveries of fledglings in July and August indicated that juveniles moved far from their natal colony shortly after fledging and before starting a true migration south (Table 1). Adults remain at their breeding colonies until fall migration or even throughout the winter (Negro et al. 1991, and unpubl. data). Two of the juveniles observed were at distances of 18 and 164 km from their natal colony 34 d and 31 d after hatching, respectively, (Table 1) supporting the hypothesis that lesser kestrel family breakup tends to take place shortly after fledging. In contrast to the black kite (*Milvus migrans*) in southern Spain in which migratory urgency determines the timing of family breakup (Bustamante and Hiraldo 1990), lesser kestrel family groups break up long before migration starts.

Lesser kestrel fledglings do not appear to participate in manipulative play with objects, or learning or practicing of hunting skills during the post-fledging dependence period in contrast to the common occurrence in most species of falcons (*Falco* spp.; e.g., Schuyt et al. 1936, Tinbergen 1940, Lawrence 1949, Cade 1953, Parker 1975, Sherrod 1983, Oliphant and Tessaro 1985, Komen and Myer 1990, Bollen 1991, Debus et al. 1991, Lawrence and Gay 1991, Varland et al. 1991). Manipulative play with objects during the post-fledging dependence period occurs more frequently in species feeding on agile prey. There is hardly any information on other raptors that feed exclusively on insects to know if it is something uncommon in insect feeders.

Adults behaved aggressively toward fledglings entering or coming near their nest and were able to recognize their offspring after fledging; i.e., banded adults were able to find their offspring among other fledglings and fed them when away from the nest. On the other hand, fledglings frequently intruded in other nests and begged from any other kestrel, resulting in the possibility that adults might accidentally feed the wrong chick (as we observed in one occasion). Before young fledge adults do not seem to be able to recognize their own offspring. When nests are connected by ledges, chicks may move between nests and accidental adoptions during the nestling period may take place (Donazar et al. 1991). While there may be an evolutionary pressure for adults to recognize their offspring and not to feed unrelated young, individual recognition takes time to develop and this would explain why nestlings apparently are not recognized. On the other hand, fledglings may obtain extra food with hardly any risk by begging from unrelated adults, explaining the lack of selectivity in their begging behavior.

ACKNOWLEDGMENTS

We are grateful to F. Hiraldo for his guidance and to M. de la Riva and Y. Menor de Gaspar for their help during the field work. E. Korpimäki, and two anonymous referees made helpful comments on a first draft of this paper. This work is part of a doctoral dissertation by J.B. at the Universidad Autónoma de Madrid. Funds were provided by project PB87-0405 DGICYT, and fellowships from the MEC and CSIC to both authors.

LITERATURE CITED

- BERNIS, F. 1980. La migración de las aves en el estrecho de Gibraltar. Vol. I. Aves planeadoras. Catedra de Zoología de Vertebrados, Univ. Complutense, Madrid, Spain.
- BESKE, A.E. 1978. Harrier radio-tagging techniques and local and migratory movements of radio-tagged juvenile harriers. M.S. thesis, Univ. Wisconsin, Stevens Point, WI U.S.A.
- BLONDEL, J. 1964. Notes sur la biologie et le régime alimentaire du Faucon crécerellette *Falco naumanni*. *Nos Oiseaux* 28:294-298.
- BOLLEN, C. 1991. Breeding behaviour and diet of the Australian kestrel (*Falco cenchroides*). *Aust. Bird Watcher* 14:44-50.
- BROWN, L. AND D. AMADON. 1968. Eagles, hawks and falcons of the world. The Wellfleet Press, Secaucus, NJ U.S.A.
- BUSTAMANTE, J. AND F. HIRALDO. 1990. Factors influencing family rupture and parent-offspring conflict in the black kite *Milvus migrans*. *Ibis* 132:58-67.
- CADE, T. 1953. Behavior of a young gyrfalcon. *Wilson Bull.* 65:26-31.
- CRAMP, S. AND K.E.L. SIMMONS. 1980. Handbook of the birds of Europe, the Middle East and North Africa. Vol. II. Oxford Univ. Press, Oxford, U.K.
- DEBUS, S.J.S., A.J. LEY, S. TREMONT AND R. TREMONT. 1991. Breeding behaviour and diet of the Australian hobby *Falco longipennis* in northern New South Wales *Aust. Bird Watcher* 14:123-137.
- DONÁZAR, J.A., J.J. NEGRO AND F. HIRALDO. 1991. A note on the adoption of alien young by lesser kestrel *Falco naumanni*. *Ardea* 79:443-444.
- KENWARD, R.E. 1978. Radio-transmitter tail-mounted in hawks. *Ornis Scand.* 9:220-223.
- KOMEN, J. AND E. MYER. 1990. Observations on post-fledging dependence of kestrels (*Falco tinnunculus ruficolus*) in an urban environment. *J. Raptor Res.* 23:94-98.
- LAWRENCE, L.K. 1949. Notes on nesting pigeon hawks at Pimisi Bay, Ontario. *Wilson Bull.* 61:15-25.
- LAWRENCE, S.B. AND C.G. GAY. 1991. Behaviour of fledgling New Zealand falcons (*Falco novaeseelandiae*). *Notornis* 38:173-182.
- NEGRO, J.J., M. DE LA RIVA AND J. BUSTAMANTE. 1991. Patterns of winter distribution and abundance of lesser kestrels (*Falco naumanni*) in Spain. *J. Raptor Res.* 25:30-35.
- , J.A. DONÁZAR AND F. HIRALDO. 1993a. Home range of lesser kestrels *Falco naumanni* during the breeding season. Pages 144-150 in M.K. Nicholls and R. Clarke [EDS.], Biology and conservation of small falcons, Proc. Hawk and Owl Trust Conf. The Hawk and Owl Trust, London, U.K.
- , ——— AND ———. 1993b. Organochlorine and heavy metal contamination in non-viable eggs and its relation to breeding success in a Spanish population of lesser kestrel *Falco naumanni*. *Environ. Pollut.* 82:201-205.

- NEWTON, I. 1979. Population ecology of raptors. T. & A.D. Poyser, Berkhamsted, U.K.
- OLIPHANT, L.W. AND S.V. TESSARO. 1985. Growth rates and food consumption of hand-raised merlins. *Raptor Res.* 19:79-84.
- PARKER, A. 1975. Young male peregrines passing vegetation fragments to each other. *Br. Birds* 68:242-243.
- POMAROL, M. 1990. Cría en cautividad y reintroducción del cernícalo primilla (*Falco naumanni*). Pages 101-117 in J.L. González and M. Merino [EDS.], El cernícalo primilla (*Falco naumanni*) en la Península Ibérica. Situación, problemática y aspectos biológicos. ICONA, Madrid, Spain.
- SCHUYL, V.G., L. TINBERGEN AND N. TINBERGEN. 1936. Ethologische Beobachtungen am Baumfalken (*Falco s. subbuteo* L.). *J. Ornithol.* 84:387-433.
- SHERROD, S.K. 1983. Behavior of fledgling peregrines. The Peregrine Fund, Inc., Ithaca, NY U.S.A.
- SIEGEL, S. AND N.J. CASTELLAN. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, Singapore.
- TINBERGEN, L. 1940. Beobachtungen über die Arbeitsteilung des Turmfalken (*Falco tinnunculus*) während der Fortpflanzungszeit. *Ardea* 29:63-98.
- VARLAND, D.E., E.E. KLAAS AND T.M. LOUGHIN. 1991. Development of foraging behavior in the American kestrel. *J. Raptor Res.* 25:9-17.
- VIÑUELA, J. AND J. BUSTAMANTE. 1992. Effect of growth and hatching asynchrony on the fledging age of black and red kites. *Auk* 109:748-757.

Received 8 November 1993; accepted 8 March 1994

HABITAT CHARACTERISTICS OF GREAT HORNED OWLS IN SOUTHCENTRAL PENNSYLVANIA

THOMAS E. MORRELL¹ AND RICHARD H. YAHNER

School of Forest Resources, The Pennsylvania State University, University Park, PA 16802-4300 U.S.A.

ABSTRACT.—We compared habitat characteristics associated with high- and low-use areas of great horned owls (*Bubo virginianus*) in forest, farm, and mixed forest-farm habitats in southcentral Pennsylvania during 1987 and 1988. High-use areas in forest habitats had a lower number ($P < 0.05$) of land-use cover types and a lower percent of deciduous forest cover than low-use areas. In farm habitats, high-use areas were significantly ($P < 0.05$) lower in elevation than low-use areas. In mixed habitats, high-use areas had a greater ($P < 0.05$) percent of cropland and pasture and lower percent of both deciduous and total forest cover than low-use areas. The overall correct classification rate in distinguishing between high- and low-use areas using stepwise logistic regression was relatively low. Stepwise logistic regression was not useful in predicting habitat characteristics important to great horned owls in each of the three habitats. Great horned owls in Pennsylvania are habitat generalists but tend to be associated with fragmented landscapes that contain nesting and foraging sites.

KEY WORDS: *Bubo virginianus*; farm habitat; forest habitat; great horned owl; habitat characteristics.

Características del hábitat de *Bubo virginianus* en el centro-sur de Pennsylvania

RESUMEN.—Comparamos características del hábitat de *Bubo virginianus* asociadas a usos alto y bajos, en bosques, áreas de cultivo y situaciones mixtas del centro-sur de Pennsylvania entre 1987 y 1988. Hábitat de bosques con áreas de alto uso tenían menor cobertura ($P < 0.05$) de otros tipos de hábitat y además tenían un porcentaje de cobertura de bosque deciduo menor que en áreas de bajo uso. En hábitat agrícolas, áreas de alto uso fueron significativamente más bajas ($P < 0.05$) en elevación que en áreas de bajo uso. En hábitats mezclados, áreas de alto uso tenían un gran porcentaje ($P < 0.05$) de cultivos y pasturas y un porcentaje de cobertura tanto de bosque deciduo como del bosque en su totalidad menor que en áreas de bajo uso. La distinción entre áreas de alto y bajo uso, usando una regresión logística paso a paso, fue relativamente baja. Este método estadístico no fue útil en predecir características de hábitat importantes para *B. virginianus*, en cada uno de los tres hábitat estudiados. *B. virginianus* en Pennsylvania hábitat-generalistas, pero tienden a estar asociados con paisajes fragmentados que contienen sitios de nidificación y forrajeo.

[Traducción de Ivan Lazo]

Populations of great horned owls (*Bubo virginianus*) have increased in some areas of Pennsylvania since the early 1970s (Goodrich and Senner 1989), but habitat use by great horned owls in Pennsylvania is poorly understood (Morrell and Yahner 1990). A better knowledge of habitat use by these owls, however, is vital to determine the influence of current and future land-use practices on population trends of this species. Land-use practices that create openings in heavily forested areas may contribute to increased numbers of great horned owls in Pennsylvania by providing foraging habitat for owls and suitable habitat for prey species (Goodrich and Sen-

ner 1989). Our objective was to compare habitat characteristics of areas receiving high and low use by great horned owls in forest, farm, and mixed forest-farm habitats of southcentral Pennsylvania.

METHODS

We conducted surveys of great horned owls along 56 16-km routes in 15 counties of southcentral Pennsylvania from early January to late May, 1987 and 1988. To select routes, 30 of 126 topographic maps (1:24 000) covering the study area were randomly selected. Two 16-km routes then were established on each map by randomly choosing a light-duty road from the map. Direction of travel along a route was selected randomly. If a route occurred within 1.6-km of another route or if it meandered excessively, it was modified or excluded to avoid covering an area more than once.

Ten stations were established at 1.6-km intervals along each survey route. Owls were surveyed by broadcasting a tape recording of the call of a "hooting" great horned owl

¹ Present address: Department of Biology, Ball State University, Muncie, IN 47306-0440 U.S.A.

Table 1. Abbreviations and description of 16 habitat characteristics used in analyses of habitat use by great horned owls in south-central Pennsylvania from January to May 1987 and 1988. Characteristics were measured within a 0.8-km radius circular plot centered on each survey station and taken from USGS 7.5-min topographic maps and aerial photographs (1:10 000).

ABBREVIATION	DESCRIPTION
COVTYPE	Number of different land-use cover types (characteristics RESID to ORCHARD below are taken from Anderson et al. [1976], see Appendix 1 for detailed descriptions of the cover types).
PATCHES	Number of individual patches of land-use cover types, where patches are defined as individual areas of a specific land-use cover type regardless of patch size that can be delineated on the aerial photographs.
INTRSPR	Index of habitat interspersation (Baxter and Wolfe 1972).
ELEV	Elevation (m) at center of the plot.
RUGGED	Index of terrain ruggedness (Beasom et al. 1983).
RESID	Percent of residential cover.
URBAN	Percent of urban cover (includes all other built-up areas other than residential).
WATER	Percent of reservoir and lake cover.
ROAD	Percent of paved road cover.
AGRIC	Percent of cropland and pasture cover.
DECID	Percent of deciduous forest cover.
CONIF	Percent of coniferous forest cover.
MIXED	Percent of mixed (combination of DECID and CONIF) forest cover.
TOTFOR	Percent of total forest cover.
RIPAR	Percent of wetland/riparian cover (includes marshes, wet meadows, streams, and rivers).
ORCHARD	Percent of orchard, grove, and vineyard cover.

(hereafter referred to as a broadcast) obtained from the Cornell Library of Natural Sounds, using a speaker-amplifier system (Perma-Power Half-Miler Hailer, Model S-610) and a portable cassette player (Realistic CTR-71). The system consisted of an 8-ohm speaker and a 40-watt amplifier. At each station, an observer exited the vehicle and listened for unsolicited owl calls (a "hooting" owl) for 2 min. The broadcast then was played for 5 min and 20 sec, during which all responding owls were recorded. A broadcast consisted of six sets of a 20-sec owl call, with each set separated by a 40-sec pause. Each set consisted of a series of four to seven note songs. The first 20-sec broadcast was made holding the speaker perpendicular to the road, with the speaker rotated 180° following each 20-sec broadcast. Immediately after the final 20-sec broadcast, 5 min were spent at the station to record locations of responding owls on a topographic map. Audio output of the playback was adjusted periodically to maintain 90–110 decibels (Fuller and Mosher 1987) as recorded by a hand-held sound meter. All surveys were conducted between 1600 and 0800 H. Surveys were not conducted when wind velocity consistently exceeded 12 km/hr (as measured with a hand-held anemometer) or when precipitation was steady.

Each survey station was classified into one of three habitats using aerial photographs (black and white, 1:10 000 scale): forest, farm, or mixed. Classification was based on vegetative and land-use cover characteristics within a 0.8-km radius circular plot centered on each survey station. When $\geq 67\%$ of the area within the radius was in forest cover, we classified the station as forest habitat. Similarly,

if $\geq 67\%$ of the area was agricultural land, the survey station was classified as farm habitat. Forest and agricultural cover were based on definitions provided by Anderson et al. (1976). When cover characteristics at a survey station did not fall into either of the above categories, it was designated mixed (forest-farm) habitat.

We used an 0.8-km radius because a vocalization of a great horned owl can be heard from a distance of up to 1 km (Rusch 1982). Thus, all owls vocalizing within the 0.8-km radius circle probably were detected. In addition, many researchers have reported that the majority of activity by great horned owls during their breeding season is confined to an area less than 0.8-km of their nest (Baumgartner 1939, Craighead and Craighead 1959, Fuller 1979, Petersen 1979). Although there may have been instances when a territory did overlap two plots, a single sample plot was sufficiently large in most cases to encompass all or most of a given territory.

We quantified 16 habitat characteristics along 34 survey routes randomly selected from the 56 survey routes (Table 1). Habitat characteristics within each 0.8-km radius were taken from aerial photographs or U.S. Geological Survey 7.5-min topographic maps and included 11 land-use cover types, two topographic features, and three measures of habitat heterogeneity. We measured each characteristic within the 0.8-km radius circular plot.

Percent of each land-use cover type (Level II, Anderson et al. 1976; Appendix 1) within a plot was determined using a Calcomp 9100 digitizer and Earth Resources Data Analysis Systems (program "Measure"). Two measures of topographic features, elevation (ELEV) and ruggedness

(RUGGED; Beasom et al. 1983), were obtained from topographic maps. Elevation (m) was recorded at the center of each 0.8-km radius circular plot. RUGGED was determined using an acetate overlay, which consisted of a uniform grid of 98 dots within the 0.8-km radius plot. The number of intersections of dots and contour lines was counted, and RUGGED was calculated as the ratio of dot-contour intersections to total number of dots ($N = 98$) in the grid.

Three measures of landscape heterogeneity used were the number of different land-use cover types (COVTYPE), number of individual patches of land-use cover type (PATCHES), and an interspersion index (INTRSPR). The number of individual patches was recorded by counting the number of patches regardless of cover type or size. We used a modified version of the Baxter-Wolfe method to obtain an interspersion index (Baxter and Wolfe 1972, Hall 1984).

The area defined within the 0.8-km radius circular plot was classified as either a high- or a low-use area by great horned owls. A high-use area was designated if two or more owl contacts occurred at the station based on the total visits combined ($N = 3-7$) to that station in a field season. A low-use area was designated if less than two owl contacts were noted during the total visits. Robbins (1970) recommended that two or more contacts of a singing bird recorded in seven visits to an area provided significant evidence for determining the presence of a breeding territory.

Habitat characteristics were compared between high- and low-use areas using single-classification analysis-of-variance and Mann-Whitney rank sums tests (Sokal and Rohlf 1981). Characteristics were compared between high- and low-use areas based on all stations combined and between high- and low-use areas based on stations in forest, farm, and mixed habitat considered separately. Normality of each characteristic was tested using the Kolmogorov D statistic and normal probability plots (SAS 1985). To test the assumption of homogeneity of variances, the folded form of the F statistic, F' , was used (SAS 1985).

Stepwise logistic regression (Dixon 1985) was used to determine which habitat characteristics best distinguished between high- and low-use areas for all stations combined and for each habitat category separately. The asymptotic covariance estimation was used to calculate F -values for entry and removal of characteristics from the models. Associated P -values for entry and removal of characteristics were 0.10 and 0.15, respectively. A characteristic was used in the regression model if comparisons between high- and low-use areas produced an F -statistic of $P < 0.10$. To reduce redundancy with other characteristics, only one pair of highly correlated ($P < 0.05$) characteristics was used in the model. However, we retained DECID for the farm habitat model because DECID was significant in segregating between high- and low-use areas in the final logistic regression models for both forest and mixed habitats.

We developed three regression models for all stations combined and for each habitat category (i.e., forest, farm, mixed). One model was developed using continuous characteristics, and two other models were developed using categorical characteristics. Two categorical models used

variables DECID and AGRIC arbitrarily separated into five (≤ 20 , 21-40, 41-60, 61-80, and $\geq 81\%$ cover) and three categories (≤ 33 , 34-66, and $\geq 67\%$ cover, respectively). Other characteristics arbitrarily separated into interval categories where ELEV (≤ 150 , 151-300, 301-450, and ≥ 451 m), RIPAR (≤ 20 and $\geq 21\%$ cover), and RUGGED (≤ 20 , 21-40, 41-60, ≥ 61) after examining the distribution of the continuous values.

RESULTS

We classified 134 (39%) and 206 (61%) of the survey stations as high- and low-use areas, respectively. One-hundred twenty-six (37%) of the 340 stations were classified as forest, 79 (23%) as farm, and 135 (39%) as mixed habitats. Fifty-nine percent of the stations in farm habitat, 43% in mixed habitat, and 23% in forest habitat were considered high-use areas.

High-use areas, based on all habitats combined, were lower in elevation (ELEV), had a greater percent of cropland and pasture cover (AGRIC), and lower percentage of both deciduous forest (DECID) and total forest cover (TOTFOR) compared to low-use areas (Table 2).

In forest habitats, high-use areas had a lower number of different land-use cover types (COVTYPE) and a lower percent of deciduous forest cover (DECID) than low-use areas (Table 2). In farm habitats, high-use areas were significantly lower in elevation (ELEV) than low-use areas. In mixed habitats, high-use areas had a greater percent of AGRIC and lower percent of both DECID and total forest cover (TOTFOR) than low-use areas.

Only three characteristics were used in the stepwise regressions for all habitats combined, and two entered the final models (Table 3). DECID and ELEV contributed significantly to the improvement of each model, but the model that used continuous characteristics provided a poor fit. The model using five categories for DECID provided the best overall correct classification.

Three characteristics also were used in the forest habitat models, but only DECID and COVTYPE were retained in the final models (Table 3). Both characteristics significantly improved the fit of the model and also improved the overall fit. The model using five categories for DECID provided the best overall fit.

Two characteristics were used in the stepwise logistic regression of farm habitat, and only ELEV entered into each of the final models (Table 3). ELEV significantly improved each model, but the overall

Table 2. Mean (\pm SE) of 16 habitat characteristics measured at high- and low-use areas ($N = 340$) of great horned owls in three habitats in south-central Pennsylvania from January to May, 1987 and 1988. Units for habitat characteristics are given in text.

HABITAT CHARAC- TERISTIC	HABITAT								
	TOTAL			FOREST			FARM		
	HIGH-USE AREA	LOW-USE AREA		HIGH-USE AREA	LOW-USE AREA		HIGH-USE AREA	LOW-USE AREA	MIXED HIGH-USE AREA
COVTYPE ^a	3.5 \pm 0.1	3.6 \pm 0.1		3.1 \pm 0.1	3.6 \pm 0.1 ^c		3.4 \pm 0.2	3.1 \pm 0.1	3.8 \pm 0.1
PATCHES ^a	10.0 \pm 0.4	9.8 \pm 0.3		8.6 \pm 0.8	9.1 \pm 0.6		8.9 \pm 0.6	9.1 \pm 0.8	11.7 \pm 0.6
INTRSPR ^a	9.1 \pm 0.3	8.9 \pm 0.3		7.5 \pm 0.7	8.1 \pm 0.5		7.5 \pm 0.6	7.7 \pm 0.8	11.1 \pm 0.5
ELEV ^a	285.5 \pm 10.3	344.0 \pm 9.9 ^c		377.9 \pm 20.3	384.1 \pm 13.7		211.9 \pm 12.2	266.3 \pm 25.2 ^c	299.0 \pm 14.8
RUGGED ^a	22.7 \pm 1.3	26.3 \pm 1.2		28.3 \pm 3.3	29.4 \pm 1.9		16.0 \pm 1.7	17.9 \pm 2.4	25.3 \pm 2.0
RESID ^b	0.3 \pm 0.1	0.7 \pm 0.2		0.3 \pm 0.2	0.5 \pm 0.2		0.3 \pm 0.2	—	0.5 \pm 0.3
URBAN ^b	0.07 \pm 0.01	0.06 \pm 0.02		—	0.1 \pm 0.1		0.2 \pm 0.1	—	—
LAKE ^b	0.3 \pm 0.2	0.3 \pm 0.1		0.03 \pm 0.04	0.3 \pm 0.2		0.02 \pm 0.02	0.1 \pm 0.1	0.6 \pm 0.5
ROADS ^b	0.5 \pm 0.1	0.5 \pm 0.1		0.5 \pm 0.1	0.7 \pm 0.1		0.3 \pm 0.1	0.2 \pm 0.1	0.4 \pm 0.1
AGRIC ^a	53.6 \pm 2.2	36.5 \pm 1.8 ^c		19.5 \pm 3.3	17.2 \pm 1.6		80.5 \pm 1.3	79.1 \pm 2.2	48.4 \pm 1.2
DECID ^a	23.6 \pm 1.9	40.4 \pm 1.9 ^c		43.7 \pm 5.6	57.4 \pm 2.7 ^c		10.4 \pm 1.2	10.0 \pm 1.7	24.3 \pm 2.5
CONIF ^b	3.7 \pm 0.5	3.6 \pm 0.4		6.5 \pm 1.6	4.1 \pm 0.6		1.0 \pm 0.2	1.3 \pm 0.5	4.3 \pm 0.7
MIXED ^a	16.9 \pm 1.7	16.6 \pm 1.3		28.3 \pm 5.8	19.1 \pm 2.2		7.0 \pm 1.1	8.8 \pm 1.6	19.3 \pm 2.3
TOTFOR ^a	44.1 \pm 2.2	60.5 \pm 1.7 ^c		78.4 \pm 3.2	80.5 \pm 1.5		18.4 \pm 1.4	20.2 \pm 2.2	47.9 \pm 1.5
RIPAR ^a	0.7 \pm 0.2	0.6 \pm 0.2		0.03 \pm 0.0	0.3 \pm 0.1		0.4 \pm 0.2	0.1 \pm 0.1	1.2 \pm 0.6
ORCHARD ^a	0.3 \pm 0.2	0.5 \pm 0.2		1.0 \pm 1.0	0.2 \pm 0.1		0.04 \pm 0.04	0.1 \pm 0.1	0.1 \pm 0.1

^a Tested with Student's *t*-test.
^b Tested with Mann-Whitney rank sum test.
^c Significant difference ($P \leq 0.05$) between high-use and low-use areas within a given habitat.

Table 3. Stepwise regression models for distinguishing habitat characteristics between high- and low-use areas of great horned owls in south-central Pennsylvania from January to May 1987 and 1988. Models were based on 133 high-use and 206 low-use areas in forest, farm, and mixed forest/farm habitats.

HABITAT	COEFFICIENT	SE OF COEFFICIENT	IMPROVEMENT CHI-SQUARE		GOODNESS-OF-FIT CHI-SQUARE		PERCENT CORRECT CLASSIFICATION	
			χ^2	P-VALUE	χ^2	P-VALUE	HIGH-USE	LOW-USE
All habitats ^a								
DECID	0.509	0.0106	34.0	0.000	62.9	0.087	66.2	67.6
ELEV	0.362	0.0148	6.2	0.013	56.8	0.180		
Constant	−1.572							
Forest ^a								
DECID	0.425	0.166	5.1	0.024	25.3	0.280	35.7	87.5
COVTYPE	0.449	0.201	5.2	0.022	20.1	0.514		
Constant	−1.572							
Farm ^b								
ELEV	0.684	0.351	4.2	0.04	7.6	0.176	93.6	25.0
Constant	−1.841							
Mixed ^a								
DECID	0.505	0.208	6.1	0.013	8.7	0.463	50.0	69.7
Constant	−0.702							

^a Model used categorical characteristics: DECID (≤ 20 , 21–40, 41–60, 61–80, and $\geq 81\%$), ELEV (≤ 150 , 151–300, 301–450, and ≥ 451 m), and RUGGED (≤ 20 , 21–40, 41–60, ≥ 61).
^b Model used categorical characteristics: DECID (≤ 33 , 34–66, and $\geq 67\%$), ELEV (≤ 150 , 151–300, 301–450, and ≥ 451 m), and RUGGED (≤ 20 , 21–40, 41–60, and ≥ 61).

fit was generally poor except for the model that used three categories for DECID. All models for farm habitat provided the same overall correct classification.

Two variables were used in the final model for mixed habitat (Table 3). AGRIC entered into the final model that used continuous characteristics, and DECID entered into the final model that used five categories for DECID and AGRIC. No characteristic was significant in distinguishing between high- and low-use areas in the model that used three categories for DECID and AGRIC. DECID significantly improved the fit of the categorical model and also provided a relatively good overall fit.

We found no significant change in any models when the variable DECID was replaced with TOTFOR. A high correlation was found between DECID and TOTFOR ($r = 0.71$, $df = 338$, $P = 0.0001$).

DISCUSSION

We did not identify habitat characteristics that were common to areas receiving high and low use in farm, forest, and mixed forest-farm habitats in southcentral Pennsylvania. High-use areas, how-

ever, had greater amounts of open cropland and pasture cover and lower amounts of deciduous and total forest cover than low-use areas, which generally was consistent with other studies. In Virginia, McGarigal and Fraser (1984) reported that great horned owls preferred old forest stands (> 80 yr old) adjacent to farmlands. In Minnesota (Fuller 1979) and Wisconsin (Petersen 1979), agricultural and undisturbed fields comprised a larger proportion of the home range of great horned owls than other habitat types because owls used fields and forest edges while foraging. Furthermore, Fuller (1979) and Petersen (1979) found that radio-tagged owls used forested habitat proportionately more often than expected based on its availability even though forested habitat comprised a relatively small proportion of the home range of an owl. Fuller (1979) cautioned that low use of a habitat, as determined by radiotelemetry, may be biologically misleading. Owls, for example, may be using an important habitat, such as an agricultural field, only to forage for prey before returning for longer periods to a different habitat, such as a woodlot containing a nest with young.

In this study, forest cover predominated on upland

ridges and agriculture was common to valleys. Thus, high-use areas were at lower elevations characterized by abundant fields and forest edges. This was especially noticeable in farm habitat where owls were often found in small woodlots along drainages and stream bottoms, which were areas lower in elevation than upland areas used for agricultural purposes. However, elsewhere agricultural areas can occur at higher elevations than forested areas (e.g., Allegheny Plateau physiographic region). Additional research is needed to determine if high-use areas in other regions are a function of the extent of farm habitat or simply due to elevational differences.

A reduced amount of deciduous forest cover in high-use than in low-use areas in both forest and mixed habitats in our study suggests that this landscape feature is important in determining habitat use by great horned owls in Pennsylvania. Petersen (1979) found that successful males (those producing >1 fledgling) used woodlots less frequently than unsuccessful males. He reasoned that a successful male spent more time in non-forested areas, such as lowland pastures and strip cover, to feed its mate and nestlings.

No difference was found in the amount of forest cover between high- and low-use areas in farm habitat, perhaps because foraging areas in farm habitats were plentiful. Thus, habitat suitability for great horned owls in farm habitat may be limited by other factors, such as the availability of adequate nesting and roosting sites. McInville and Keith (1974) and Baumgartner (1939) suggested that habitat suitability for great horned owls may depend on number and proximity of open non-forested areas. Craighead and Craighead (1959) reported that the distribution of suitable woodlots (>4.0 ha) determined the distribution and density of great horned owls in Wisconsin and all woodlots containing nesting owls had extensive proximal non-forested uncultivated land.

One possible explanation why few habitat characteristics distinguished between high- from low-use areas is that great horned owls may select territories based on characteristics not measured in our study. For example, we did not quantify prey densities and distribution, but these may be important to habitat selection by some owls (Adamcik et al. 1978). Moreover, perhaps methods used in our study to measure habitat characteristics may not provide an accurate assessment of the habitat or were not precise enough to show differences in habitats that great horned owls perceive as being biologically important.

In summary, we conclude that great horned owls in Pennsylvania are habitat generalists. Factors influencing habitat use by great horned owls may simply be a suitable nesting site that is adjacent to open non-forested areas used for foraging. We recommend that other studies evaluate characteristics of great horned owls on a smaller sampling area (e.g., 0.4-km radius) than that used in our study. Perhaps a smaller sampling area would provide a better indication of habitat use by an owl because a larger sampling area increases the possibility of including non-use areas within a high-use survey plot. In addition, non-significant characteristics that occurred infrequently in our study (e.g., urban, roads, orchard) should be eliminated from consideration as important owl habitat characteristics in future studies.

ACKNOWLEDGMENTS

Financial support for this project was provided by the Pennsylvania Game Commission, the National Rifle Association, the Western Pennsylvania Conservancy, the Pennsylvania Agricultural Experiment Station, the Max McGraw Wildlife Foundation, and the Hawk Mountain Sanctuary Association. We thank M.J. Batchelor, C.M. Butchkowski, J.P. Dunn, K.W. Eakin, B.J. Dickinson, and R.A. Voytko for field assistance; W.L. Harkness for statistical advice; W.M. Tzilkowski for computer assistance; B.J. Burhans and T.L. Yarrington for assistance with quantifying remote-sensing data; J.F. Karish and H.J. Greenlee of the National Park Service at Gettysburg National Military Park for logistical support; and J.D. Hassinger of the Pennsylvania Game Commission for his cooperation with all phases of the project.

LITERATURE CITED

- ADAMCIK, R.S., A.W. TODD AND L.B. LLOYD. 1978. Demographic and dietary responses of great horned owls during a snowshoe hare cycle. *Can. Field-Nat.* 9: 156-166.
- ANDERSON, J.R., E.E. HARDY, J.T. ROACH AND R.E. WITMER. 1976. A land use and land cover classification system for use with remote sensor data. U.S. Geol. Surv. Prof. Pap. 964. Washington, DC U.S.A.
- BAUMGARTNER, F.M. 1939. Territory and population in the great horned owl. *Auk* 56:274-282.
- BAXTER, W.L. AND C.W. WOLFE. 1972. The interdispersion index as a technique for evaluation of bobwhite quail habitat. Pages 158-165 in J.A. Morrison and J.C. Lewis [Eds.], *Trans. First Quail Symp.* Oklahoma State Univ., Stillwater, OK U.S.A.
- BEASOM, S.L., E.P. WIGGERS AND J.R. GIARDINO. 1983. A technique for assessing land surface ruggedness. *J. Wildl. Manage.* 47:1163-1166.
- CRAIGHEAD, J.J. AND F.C. CRAIGHEAD. 1959. *Hawks, owls, and wildlife.* Stackpole, Harrisburg, PA U.S.A.

DIXON, W.J. [ED.]. 1985. BMDP statistical software. Univ. California Press, Berkeley, CA U.S.A.

FULLER, M.R. 1979. Spatiotemporal ecology of four sympatric raptor species. Ph.D. dissertation. Univ. Minnesota, Minneapolis, MN U.S.A.

——— AND J.A. MOSHER. 1987. Raptor survey techniques. Pages 37–65 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC U.S.A.

GOODRICH, L.J. AND S.E. SENNER. 1989. Recent trends of wintering great horned owls (*Bubo virginianus*), red-tailed hawks (*Buteo jamaicensis*) and two of their avian prey in Pennsylvania. *J. Pa. Acad. Sci.* 62:131–137.

HALL, P.A. 1984. Characterization of nesting habitat of goshawks (*Accipiter gentilis*) in northwestern California. M.S. thesis, Humboldt State Univ., Arcata, CA U.S.A.

MCGARIGAL, K. AND J.D. FRASER. 1984. The effects of forest stand age on owl distribution in southwestern Virginia. *J. Wildl. Manage.* 48:1393–1398.

MCINVAILLE, W.B. AND L.B. KEITH. 1974. Predator-prey relations and breeding biology of great horned owls and red-tailed hawks in central Alberta. *Can. Field-Nat.* 88:1–20.

MORRELL, T.E. AND R.H. YAHNER. 1990. Status and habitat characteristics of the great horned owl in Pennsylvania. Final Rep., School of Forest Resources, Pennsylvania State Univ., University Park, PA U.S.A.

PETERSEN, L. 1979. Ecology of great horned owls and red-tailed hawks in southeastern Wisconsin. Wisconsin Dept. Nat. Resour. Tech. Bull. No. 111. Madison, WI U.S.A.

ROBBINS, C.S. 1970. Recommendations for an international standard for a mapping method in bird census work. *Audubon Field Notes.* 24:723–726.

RUSCH, D.H. 1982. Great horned owl. Pages 87–88 in D.E. Davis [ED.], CRC handbook of census methods for terrestrial vertebrates. CRC Press Inc., Boca Raton, FL U.S.A.

SAS INSTITUTE INC. 1985. SAS User's guide: statistics, version 5 edition. Cary, NC U.S.A.

SOKAL, R.R., AND F.J. ROHLF. 1981. Biometry. W.H. Freeman, San Francisco, CA U.S.A.

Received 14 June 1993; accepted 8 May 1994

Appendix 1. Definitions of characteristics used to define land-use cover types in south-central Pennsylvania, 1987 and 1988. Definitions are modified Level-II classifications (Anderson et al. 1976).

CHARACTERISTIC	DEFINITION
RESID	Areas of occupied dwellings ranging from high-density (multiple-unit structures of urban cores) to low-density (houses are on lots of more than an 0.4 ha on the periphery of urban expansion). Linear residential developments along transportation routes are included.
URBAN	Includes all other built-up areas of intensive use, including towns, cities, strip developments, shopping and industrial centers, mills, institutions, commercial complexes, mining operations, cemeteries, waste dumps, ski areas, railroad transportation routes, airports, quarries, strip mines, and all areas of open land that are intensively used, such as parks and golf courses. Included in the above definition are some characteristics defined as Other Urban or Built-up Land by Anderson et al. (1976).
ROAD	All paved roads that are two lanes or wider.
CROP	All land used primarily for the purposes of cropland and pasture.
ORCHARD	Includes orchards, groves, and vineyards. Tree nurseries and plantations were included in this cover type in our study.
WATER	Bodies of water that, if linear, are at least 0.20-km wide and, if extended, cover at least 16 ha or areas of water that are non-flowing, naturally enclosed bodies of water (including islands too small to delineate), and artificial impoundments of water used for irrigation, recreation, hydroelectric power generation. Lakes and reservoirs are classified separately by Anderson et al. (1976), but as one cover type for our study.
DECID	All forested areas having a predominance of trees (i.e., >67%) that lose leaves at the end of the frost-free season or at the beginning of the dry season.
CONIF	All forested areas having a predominance of trees (i.e., >67%) that remain green throughout the year.
MIXED	All forested areas having an intermixture (33–67%) of both coniferous and deciduous trees.
RIPAR	Includes wet meadows, bogs, or swamps, and seasonally wet or flooded basins, playas, or pot-holes with no surface-water outflow. Also included are streams and rivers where the water course is uninterrupted by a control structure. Riparian includes streams and rivers as defined by Anderson et al. (1976), who defines each separately.

PARENT-OFFSPRING RELATIONS DURING THE POST-FLEDGING DEPENDENCY PERIOD IN THE BLACK KITE (*Milvus migrans*) IN JAPAN

KIMIYA KOGA AND SATOSHI SHIRAISHI¹

Zoological Laboratory, Faculty of Agriculture, Kyushu University 46-06, Fukuoka 812, Japan

ABSTRACT.—The transition to independence of the juvenile black kite (*Milvus migrans*) was investigated in four families near the tip of Nagasaki Peninsula in Japan, where the kite is resident. The juveniles fledged at 58–63 d of age, and they became independent at 46.8 d on average after fledging. The frequency of begging and approaches by the juvenile toward the parents did not change through the post-fledging dependency period. With respect to parental effort, the frequency of parental approaches toward the juvenile and the parental feeding frequency decreased with juvenile age. Furthermore, the parents in the two families studied in detail avoided juvenile approaches, and the female parent of one family dived her offspring two d before juvenile independence. Thus, the parents decreased the parental care over time. This suggests that decreases in parental effort are related to the juvenile independence of the resident black kite.

KEY WORDS: *black kites; juvenile independence; Milvus migrans; parental care; post-fledging dependency period.*

Relación padre-cría durante el período de dependencia post-volantón en *Milvus migrans* en Japón

RESUMEN.—Se estudió la transición a la independencia en los juveniles de *Milvus migrans* de cuatro familias, cerca del extremo de la península de Nakasaki en Japón, donde esta ave es residente. Los volantones juveniles de 58 a 63 días de edad, llegaron a ser independientes en un promedio de 46.8 días, después de volar. La frecuencia con la que los juveniles se acercaron a sus padres para pedir alimento no cambia a través del período de dependencia post-volantón. Respecto al esfuerzo parental, estos disminuyeron la frecuencia de alimentación a los juveniles a medida que aumentaba su edad. Así, el cuidado parental decrece en el tiempo, patrón que puede estar relacionado con la subsecuente independencia de los juveniles.

[Traducción de Ivan Lazo]

In many bird species, juvenile birds depend on their parents for some period even after leaving the nest (Ashmole and Tovar 1968, Alonso et al. 1987, Kopachena and Falls 1993 and references therein). Relations between parents and offspring during this transition to independence have been studied in some raptors. According to these studies, the independence of juveniles is brought about largely by parental aggression toward juveniles (Alonso et al. 1987; *Aquila heliaca*), by decreasing parental efforts toward juveniles (Wyllie 1985; *Accipiter nisus*, Ceballos and Donázar 1990; *Neophron percnopterus*), or abrupt dispersal of juveniles still under parental care (Walker 1987; *Aquila chrysaetos*). A breakup of a family tie is influenced by migration in European breeding populations of black kites (*Milvus migrans*), which

winter in Africa (Bustamante and Hiraldo 1990). In Japan, however, the black kite is resident. Therefore, one can expect either of the following transitions to juvenile independence: (1) parents initiate the process (e.g., by parental aggression or a reduction in parental effort), or (2) juveniles become independent without a decrease in parental care. The purpose of this study is to examine parent-offspring relations during the post-fledging dependency period in the resident black kite, and to describe the factors leading to juvenile independence.

MATERIALS AND METHODS

During June–August of 1986, 1991 and 1992, four families (families A and B in 1986, family C in 1991, and family D in 1992) were studied near the tip of Nagasaki Peninsula (32°30'N, 129°45'E). In this study area, pairs of kites maintain their territories through the year (Koga and Shiraishi 1994). Since the above four families occupied their territories at separate sites, we regarded these pairs as different. The topographic relief is relatively steep with

¹ Author to whom reprint requests should be sent.

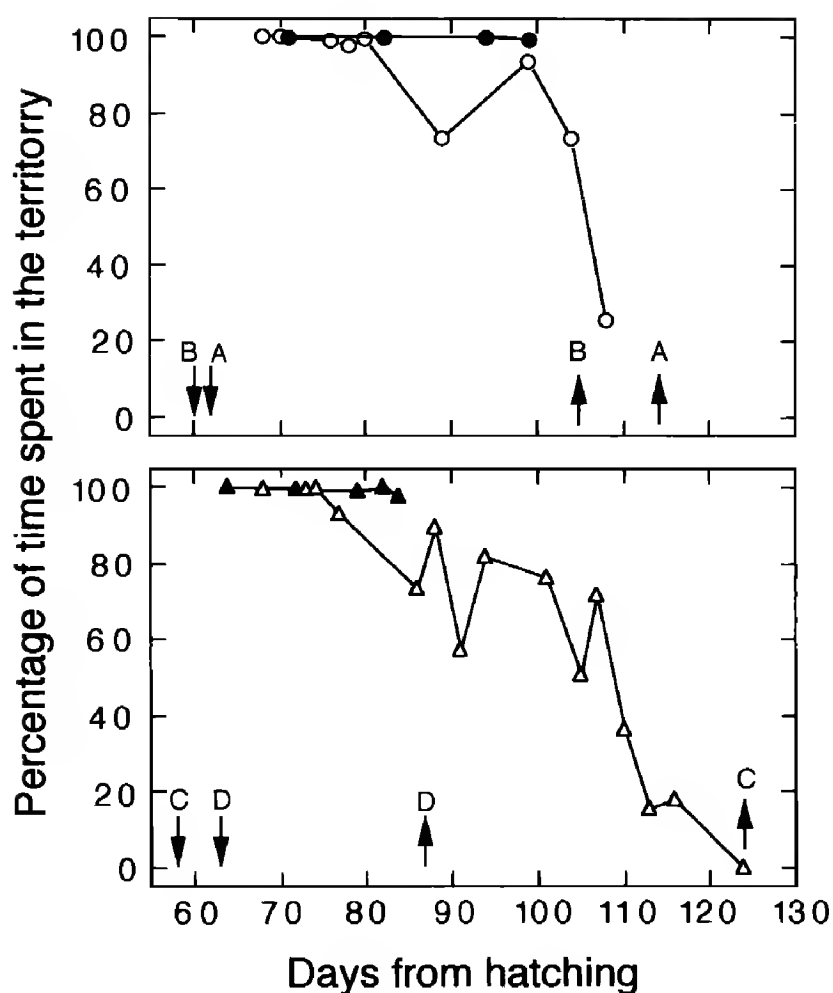


Figure 1. Percentage of time the juveniles spent in the natal territories, according to age of the first hatched young. ○—○, the juvenile of family A; ●—●, the juvenile of family B; △—△, the juvenile of family C; ▲—▲, the juvenile of family D. Fledging age is represented by (↓) and independent age by (↑). A—D represents the juveniles of families A—D, respectively.

an elevation of ca. 200–260 m. The main tree species in the study area are *Castanopsis cuspidata* and *Quercus glauca*, with small stands of *Q. acutissima*. In this area, black kites usually foraged in two fishing ports (about 3 km away) and on coasts or shores, and breeding individuals defended a radius of ca. 50–100 m centered on their nesting trees.

The date when the first egg was laid was 4 March in family A, 10 March in family B, 21 March in family C and 1 April in family D. The clutch size was two in families A and C, and one in family D. One nestling hatched in families A, B, and D, two nestlings hatched in family C, and all nestlings fledged. All the nestlings studied were radiotagged and marked with a colored band about 10 d prior to fledging. The nestling of family D was also fitted with a colored tail streamer (Konrad and Gilmer 1986). Nestlings of families A and B were fitted with radiotransmitters (50–53 MHz range) attached by a backpack harness (Kenward 1985). The transmitter and harness weighed approximately 30 g (ca. 3% of the body weight). Because the transmitters failed ca. 3 wk after the attachment, data on activities of the juveniles out of their natal territories were not obtained. Nonetheless, transmitters were useful markers for individual identification

during watching in the territories. Juveniles of families C and D had transmitters operating in the 144–146 MHz range (ca. 14 g, Architect Co., Tokyo) attached to their backs with a fast-drying glue. Sex distinction and individual identification of the parent birds were based on the color of body feathers (usually light in males, and dark in females) and the plumage characters (e.g., slightly different patterns of the breast feathers, white feathers around the base of the bill, or broken flight feathers), respectively.

Field work started after fledging (ranging from mid-June to early July), and it was ended when the juveniles became independent: the day of independence was defined as the first time that the juveniles were not seen in the natal territories during observation. In families A and B, a half-day observation was made 5 and 10 d after independence, and the juveniles were not found in their natal territories. In family C, the elder juvenile provided all its own food and roosted out of the territory before the independence day (see the Results section for the death of its younger sibling). The juvenile of family D was pursued on the first and fifth days after it left the home territory, and then radio signals were monitored around the territory every morning and evening for about a month. As a result, it seemed that the juvenile did not return to the parental territory, although it suddenly appeared near the natal territory 25 d after independence. Thus, our definition of independence may be acceptable.

On rainy days observations were not carried out because of difficulty in the identification of wet individuals. In our study area the rainy season extended from mid-June to mid-July. Consequently, intervals between observations were irregular (2–14 d, see Fig. 1). Observations were made through binoculars (8 × 30) and a telescope (25–40×). The duration of each observation was 5–7 hr between 0600 and 1900 H in families A and B, and 13–14.5 hr (from dawn until dusk) in families C and D. The number of observation bouts was nine in family A (49 hr), four in family B (24 hr), 16 in family C (221.6 hr), and seven in family D (98.1 hr).

Observed behaviors were recorded in a notebook in as much detail as possible or recorded on a tape recorder. The locations of the juveniles in families C and D were determined visually, then plotted on a map of a scale of 1:2500 or 1:25 000. If visual contact was lost, the juveniles were located by radio-triangulation. The daily total of durations of visual contact with the juveniles in families C and D was at least 522 min and usually more than 700 min. In the present analysis of parent-offspring relations, the following measures were used as variables indicating juvenile interest in maintaining contact with the parents, parental interest in maintaining contact with the juveniles, and parental effort to care for the juveniles.

Juvenile Interest. (1) Frequency of approaches by the juvenile (FAJ) toward the parents when at least one parent and the juvenile were present together (times/hr). A juvenile approach occurred when the juvenile flew to the parent(s) and landed usually ≤ 1 m of them. (2) Frequency of begging by the juvenile (FAB) when at least one parent and the juvenile were present together (times/hr). We regarded each behavioral sequence comprising various consecutive begging and silent periods as one begging activity. If different behaviors (e.g., preening) were observed

Table 1. The number of samples used for analyses of each variable.^a

FAMILY	FAJ	FBJ	FAP	NPE/FAJ	NPF	TSJ	TSP	TSF	HRS
A	9	9	9	— ^b	9	9	9	— ^c	— ^c
B	4	4	4	— ^b	4	4	4	— ^c	— ^c
C	14 ^d	14 ^d	14 ^d	12 ^e	16	16	9 ^f	12 ^f	12 ^f
D	5	5	5	5	5	5	5	7 ^g	7 ^g

^a See Materials and Methods for abbreviations.

^b The analysis was not conducted, owing to a small number of juvenile approaches (in many cases, less than three times per observation bout).

^c The sufficient data were not obtained, because of failure in transmitters.

^d The data from two observation bouts were omitted from the analysis, because the parents and juvenile were not present together.

^e The data from four observation bouts near the independent day were not used, owing to a small number of juvenile approaches (less than three times per observation bout).

^f Since it was impossible that the juvenile flight activities (TSF and HRS) and TSP near juvenile independence were measured at the same day, the sample sizes of these variables were smaller than the number of observations.

^g The data from two observation bouts after independence were added, to estimate the development of the flight ability more correctly

between two such begging sequences, we considered each begging activity to be a separate one.

Parental Interest. (3) Frequency of approaches (FAP) by the parent toward its juvenile when at least one parent and the juvenile were present together (times/hr). When the parent flew to a juvenile and landed within 1 m of it, we considered this to be a parental approach. (4) The ratio of the number of parental escapes from the juvenile (NPE) to that of juvenile approaches (FAJ). A parental escape occurred if the parent left a tree just before or ≤ 30 sec after the juvenile landed near the parent.

Parental Effort. (5) The number of parental feedings (NPF) per young per hr. We regarded as parental feedings when the parents tore prey and offered pieces of meat to the juveniles, when the parents transferred prey to their offsprings, or when the juveniles snatched prey held by the parents on a branch. Feeding of an unmarked, begging juvenile was observed twice 11 d after fledging of the first hatched young in family C. Although such feedings might make the adults waste their time and energy, we omitted these feedings from our data.

In addition to these variables, the total time spent by both the juvenile (TSJ) and at least one parent (TSP) in the parental territory was also recorded. Furthermore, the daily amount of time spent in flying by the juveniles (TSF) of families C and D was examined, and their home range sizes (HRS) were estimated using the minimum polygon method.

Since the first author conducted observations by himself, it was impossible to monitor simultaneously the behavior of the parents in the vicinity of the nest and that of the juvenile outside the territory. Moreover, in several observation bouts of family C, the parents and juvenile were not present together, or the number of juvenile approaches during watching was too small to create detectable changes in the ratio of NPE/FAJ. Consequently, the number of samples used for analyses of some variables in family C was smaller than that of observations conducted (Table 1). In family D, TSFs and HRSs were examined for additional days after independence to estimate the development of the flight ability more accurately.

For each family, we calculated simple linear regression correlation coefficients between age of the first hatched young and each of the variables. Further, to examine the relationship between age and each of the variables used to describe parent-offspring relations (FAJ, FBJ, FAP, NPE/FAJ and NPF) for all the families pooled together, we calculated partial correlation coefficients using multiple regression models of the form $Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2$, where Y was each of the five variables all of which were standardized, β_0 was a constant, β_1 was the coefficient for standardized age of the first juvenile (X_1), β_2 was the coefficient for the family groups (X_2) that were assigned scores. The scores were calculated using the following equation: $Sc = Ni - S/F$, where Sc was the score, Ni was the number of observation bouts in family i , S was the sum of all Ni , and F was the number of families examined. Correlation coefficients were computed also between age and logarithmic-transformed data on TSFs and HRSs for the juveniles of families C and D. Statistical significance was set at 0.05. Means were expressed with SD.

RESULTS

Activities of the Juveniles. Young black kites fledged at 58–63 d. The younger juvenile of family C died of unknown reason 25 d after fledging (83 d of age). Therefore, the analysis of juvenile activities in this family was based on the data obtained from the elder juvenile. The juveniles of families A, B and D became independent at 114, 105 and 87 d of age, respectively. The elder juvenile of family C attended the communal roost out of its home territory at 111 d of age, and then spent most time in resting and soaring out of the natal territory. This juvenile did not appear in the parents' territory on 124 d of age. The average length of the post-fledging dependency period was 46.8 ± 17.5 d ($N = 4$).

Table 2. Simple or partial correlation coefficients (*r*) between the age in days of young and the variables concerning the parent-offspring relation.

VARIABLE ^a	FAMILY	<i>r</i>	RANGE	PROBABILITY
FAJ	A	0.118	0–1.62	0.762
	B	0.936	0.31–0.53	0.064
	C	0.413	0.28–1.63	0.142
	D	0.328	0.44–0.91	0.590
	pooled	0.232	–1.33–1.99	0.209
FBJ	A	0.447	0–4.00	0.228
	B	–0.311	0.33–0.92	0.689
	C	0.180	0.59–2.90	0.539
	D	0.473	1.38–2.66	0.421
	pooled	0.04	–1.45–2.60	0.831
FAP	A	–0.693	0–1.25	0.039
	B	–0.972	0.52–0.92	0.028
	C	–0.927	0–0.84	<0.001
	D	–0.921	0.07–0.42	0.027
	pooled	–0.649	–1.05–2.44	<0.001
NPF/FAJ	C	0.968	0–1.00	<0.001
	D	0.908	0.27–0.67	0.033
	pooled	0.962	–1.74–1.51	<0.001
NPF	A	–0.652	0–0.80	0.057
	B	–0.030	0.35–0.67	0.970
	C	–0.833	0–0.63	<0.001
	D	–0.857	0.14–0.63	0.070
	pooled	–0.659	–1.31–1.95	<0.001

^a See Materials and Methods for abbreviations.

In families A and B, the juveniles did not forage during observation, but the 82-d-old juvenile of family B plucked leaves from a tree twice while in flight. In the family C juvenile, such a plucking behavior was occasionally observed from 86–105 d old (*N* = 15). This juvenile began foraging at 101 d of age, and captured 13 prey by itself during observations. The juvenile of family D was once observed plucking leaves 83 d after hatching. On the same day the juvenile picked up and ate one earthworm, yet it apparently depended on its parents for almost all food until it became independent.

Sufficient data on the development of flying ability were obtained only from the two juveniles of families C (the elder juvenile) and D, owing to failure in transmitters of the juveniles in families A and B and to the death of the younger juvenile in family C. TSFs of the elder juvenile in family C varied from 0.5–12 min before 74 d of age, and then increased

(303 min at the maximum, *r* = 0.83, *df* = 10, *P* < 0.01). The juvenile of family D devoted 4–14 min to flying until 82 d of age, and then increased TSFs (294 min at the maximum, *r* = 0.89, *df* = 5, *P* < 0.005). HRSs of these two juveniles also increased exponentially with their age (the juvenile of family C ranged from 0.05–423.5 ha, *r* = 0.94, *df* = 10, *P* < 0.001, and the juvenile of family D ranged from 0.7–119.5 ha, *r* = 0.792, *df* = 5, *P* = 0.034).

TSJs in families A and C decreased with age (family A, *r* = –0.77, *df* = 7, *P* = 0.014; family C, *r* = –0.940, *df* = 14, *P* < 0.001; Fig. 1). In contrast, the juveniles of families B and D devoted all or almost all of their time in their parents’ territories until they gained full independence (family B, *r* = –0.66, *df* = 2, *P* = 0.336; family D, *r* = –0.591, *df* = 3, *P* = 0.249). FAJs and FBJs were not correlated with age even when each juvenile was considered separately (Table 2), indicating that the juvenile solicitation for food and juvenile interests in the parents did not decrease through the post-fledging dependency period.

Activities of the Parents. The parents of all the four families roosted in their territories during the study period. In families A and C, TSPs tended to decrease through the post-fledging dependency period (family A, *r* = –0.85, *df* = 7, *P* = 0.004; family C, *r* = –0.85, *df* = 7, *P* = 0.004), although a slight increase occurred around juvenile independence (Fig. 2). In contrast, there was no relationship between TSPs and juvenile age in families B and D (family B, *r* = –0.60, *df* = 2, *P* = 0.403; family D, *r* = –0.43, *df* = 3, *P* = 0.472). Nevertheless, the parents of the family B evidently decreased the time spent in its territory just before the juvenile independence.

Although both parents carried food for their juveniles, the male parent delivered most of the prey to the juveniles (males, 0.32 ± 0.11 prey/hr, *N* = 4; female, 0.04 ± 0.02 prey/hr, *N* = 4). The parents usually carried prey to the place where the juvenile perched (family A, *N* = 15; family B, *N* = 11; family C, *N* = 51; family D, *N* = 11), while the juvenile occasionally flew to the place where the parent landed with food (family A, *N* = 2; family B, *N* = 1; family C, *N* = 15; family D, *N* = 15). In family C, NPFs decreased with juvenile age (Table 2). NPFs in families A and D also tended to decrease during the post-fledging dependency period, although this tendency was not significant. When data from all of the pairs were pooled, a decrease in NPFs was apparent. The parents of families A and C stopped feeding 1 and 2 wk before the juvenile independence,

respectively. FAPs significantly decreased through time, even when each pair was considered separately. The avoidance of juveniles by parents was examined in families C and D in which the juveniles approached their parents more frequently than in the other two families. The ratio of NPE/FAJ was positively correlated with juvenile age. These results suggest that the effort of parental care decreased gradually during the post-fledging dependency period.

In families A, B and C, there was no evidence that the parents attacked their juveniles. In contrast, the female parent of Family D made steep dives (four occasions) at her juvenile 2 d before juvenile independence (85 d of age), when the juvenile began to increase its flying activities. Three of these dives occurred in succession when both the female parent and her juvenile soared together within the home territory. The fourth dive was directed at her juvenile perching on a branch. During these dives, the male remained perched on a branch and silently watched.

DISCUSSION

As observed in other birds (Morehouse and Brewer 1968, Moreno 1984, Alonso et al. 1987, Lett and Bird 1987, Ceballos and Donazar 1990), black kites, migrating from Europe to Africa, decrease the frequency of parental feeding around juvenile independence (Bustamante and Hiraldo 1990). However, because the decline in the feeding frequency is slight (a decrease of only 0.3 feedings/day, using the equation fitted by Bustamante and Hiraldo (1990)), reduction of parental effort is not a determining factor that leads to independence. It has been suggested that the initiation of migration influences a rupture of family ties (Bustamante and Hiraldo 1990). On the other hand, although the juveniles of Japanese black kites continued to solicit parental care through the post-fledging dependency period, the parents evidently reduced NPFs. In the absence of measurements of weight loss by the juveniles, this finding is not direct evidence that the juveniles did not receive sufficient food. However, in two families the parents cut off feeding. Furthermore, a decrease in FAPs in all the four families and an increase in the ratio of NPE/FAP in the two investigated families indicate that the parents became reluctant to look after their juveniles with time. Additionally, in one family juvenile independence occurred 2 d after parental aggression. Thus, our observations suggest that the juvenile independence in the resident black kite may be encouraged by decreased parental effort.

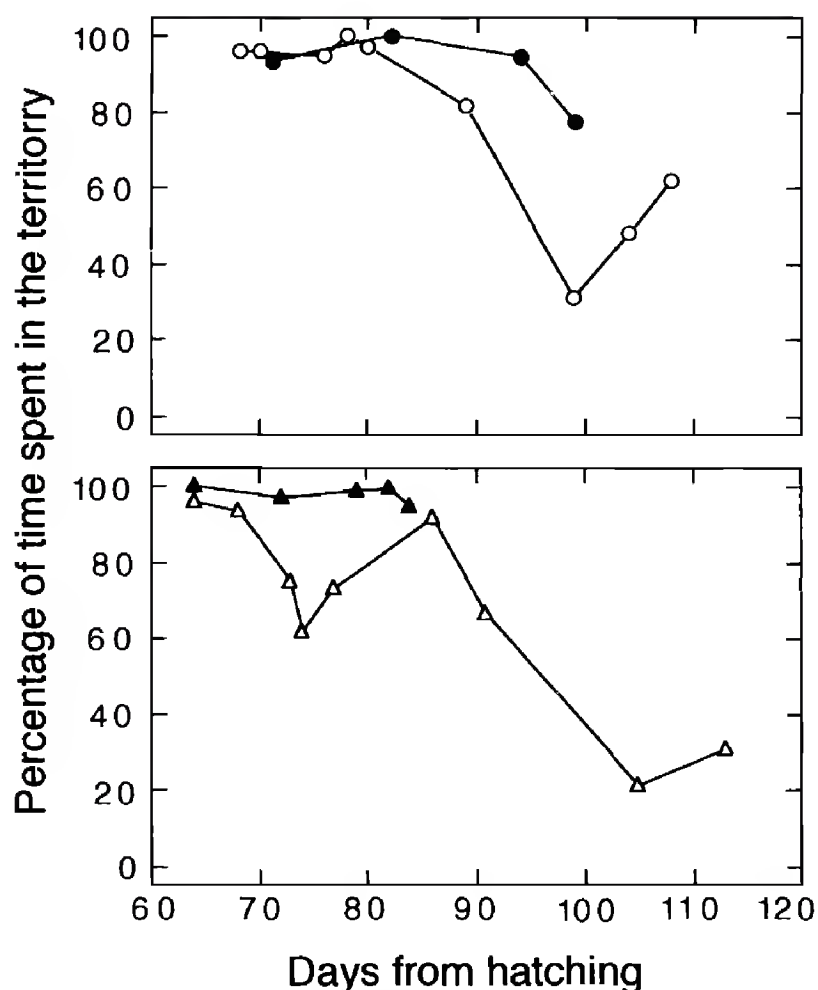


Figure 2. Percentage of time at least one parent spent in the territories, according to age of the first hatched young. ○—○, the parents of family A; ●—●, the parents of family B; △—△, the parents of family C; ▲—▲, the parents of family D.

In black-capped chickadees (*Parus atricapillus*), parental aggression has been interpreted as a behavior to encourage juveniles to feed independently (Leonard et al. 1991). Davies (1976, 1978) has shown that in two passerine species juveniles become independent when they can obtain food more efficiently by self-feeding than by begging from their parents which decrease feeds. In contrast to this, it has been suggested that independence in marsh tits (*Parus palustris*) is initiated by juveniles themselves because it is more likely that juveniles dispersing earlier obtain territories as adults (Nilsson and Smith 1985, Nilsson 1990). Kenward et al. (1993) have indicated that juvenile goshawks (*Accipiter gentilis*) may disperse abruptly after maturation of hunting behavior, for there may be little advantage for juveniles to remain where there is an adult pair because of low adult mortality and decreasing food availability. In resident black kites the juveniles might not have pressure to leave the parents' territories early, unlike marsh tits and goshawks, because kites probably start to breed at 2–3 yr of age (Newton 1979), and

in our study area the birds fed mainly on discarded fish which obviously does not require complex capture techniques. On the other hand, such food habits may allow the parents to end their parental care without giving a serious disadvantage to the juveniles in flying ability.

Parents and offspring are expected to disagree about the amount of parental investment, and overt conflicts between them are predicted (Trivers 1974). As considered in other birds (Davies 1978, Alonso et al. 1987, Hiraldo et al. 1989, Ceballos and Donazar 1990), it is possible that parental aggression and decreased parental effort in black kites may be related to this parent-offspring conflict (but see Mock and Forbes 1992). However, the level of begging by juvenile black kites tended to be unchanged during the post-fledging dependency period, which is not consistent with the expectation from Trivers' theory, i.e., juveniles should solicit food more intensively when parents withhold prey. Since parental and juvenile behaviors are influenced also by various factors unrelated to parent-offspring conflict (see Clutton-Brock 1991, Mock and Forbes 1992), further studies are required in order to show whether parent-offspring conflict exists in this species.

In conclusion, although our results based on only four families should be regarded as preliminary, they suggest that decreases in parental effort may be the main factor which leads the juvenile to independence in the resident black kite.

ACKNOWLEDGMENTS

We are grateful to E.W. Jameson, Jr. and T. Mōri for valuable comments on the early draft of this manuscript; T. Yanagawa and M. Shimojo for statistical advice and analysis; T. Senta, O. Tabeta, and A. Ishimatsu, for a variety of kindnesses; and graduate students of our laboratory and of Nagasaki University for help with capture of kites. We also thank D. Mock and an anonymous reviewer for reading and providing helpful and constructive comments on the manuscript. This study was supported in part by a Grant-in-Aid for Encouragement of Young Scientists (to K. Koga) from the Japan Ministry of Education, Science and Culture. Koga was also supported partially by a JSPS Fellowship for Japanese Junior Scientists.

LITERATURE CITED

- ALONSO, J.C., L.M. GONZALEZ, B. HEREDIA AND J.L. GONZALEZ. 1987. Parental care and the transition to independence of Spanish imperial eagles *Aquila heliaca* in Doñana National Park, southwest Spain. *Ibis* 129: 212-224.
- ASHMOLE, N.P. AND S.H. TOVAR. 1968. Prolonged parental care in royal terns and other birds. *Auk* 85:90-100.
- BUSTAMANTE, J. AND F. HIRALDO. 1990. Factors influencing family rupture and parent-offspring conflict in the black kite *Milvus migrans*. *Ibis* 132:58-67.
- CEBALLOS, O. AND J.A. DONÁZAR. 1990. Parent-offspring conflict during the post-fledging period in the Egyptian vulture *Neophron percnopterus* (Aves, Accipitridae). *Ethology* 85:225-235.
- CLUTTON-BROCK, T.H. 1991. The evolution of parental care. Princeton Univ. Press, Princeton, NJ U.S.A.
- DAVIES, N.B. 1976. Parental care and the transition to independent feeding in the young spotted flycatcher (*Muscicapa striata*). *Behaviour* 59:280-295.
- . 1978. Parental meanness and offspring independence: an experiment with hand-reared great tits *Parus major*. *Ibis* 120:509-514.
- HIRALDO, F., M. DELIBES AND R.R. ESTRELLA. 1989. Observations of a zone-tailed hawk family during the post fledging period. *J. Raptor Res.* 23:103-106.
- KENWARD, R.E. 1985. Raptor radio-tracking and telemetry. Pages 409-420 in I. Newton and R.D. Chancellor [EDS.], Conservation studies on raptors, ICBP Tech Publ. No. 5. International Council for Bird Preservation, Cambridge, U.K.
- , V. MARCSTRÖM AND M. KARLBOM. 1993. Post-nestling behaviour in goshawks, *Accipiter gentilis*: I. The causes of dispersal. *Anim. Behav.* 46:65-370.
- KOGA, K. AND S. SHIRAISHI. 1994. Copulation behaviour of the black kite *Milvus migrans* in Nagasaki Peninsula. *Bird Study* 41:29-36.
- KONRAD, P.M. AND D.S. GILMER. 1986. Post fledging behavior of ferruginous hawks in North Dakota. *Raptor Res.* 20:35-38.
- KOPACHENA, J.G. AND J.B. FALLS. 1993. Postfledging parental care in white-throated sparrow (*Zonotrichia albicollis*). *Can. J. Zool.* 71:227-232.
- LEONARD, M.L., A.G. HORN AND L.M. RATCLIFFE. 1991. Parental aggression in black-capped chickadees. *Behav. Ecol.* 2:228-233.
- LETT, D.W. AND D.M. BIRD. 1987. Postfledging behavior of American kestrels in southwestern Quebec. *Wilson Bull.* 99:77-82.
- MOCK, D.W. AND L.S. FORBES. 1992. Parent-offspring conflict: a case of arrested development. *Trends Ecol. Evol.* 7:409-413.
- MOREHOUSE, E.L. AND R. BREWER. 1968. Feeding of nestling and fledgling eastern kingbirds. *Auk* 85:44-54.
- MORENO, J. 1984. Parental care of fledged young, division of labor, and the development of foraging techniques in the northern wheatear (*Oenanthe oenanthe* L.) *Auk* 101:741-752.
- NEWTON, I. 1979. Population ecology of raptors. T. & A.D. Poyser, Calton, U.K.

- NILSSON, J.-Å. 1990. Family flock break-up: spontaneous dispersal or parental aggression? *Anim. Behav.* 40:1001–1003.
- AND H.G. SMITH. 1985. Early fledgling mortality and the timing of juvenile dispersal in the marsh tits *Parus palustris*. *Ornis Scand.* 16:293–298.
- TRIVERS, R.L. 1974. Parent-offspring conflict. *Am. Zool.* 14:249–264.
- WALKER, D.G. 1987. Observations on the post-fledging period of the golden eagle *Aquila chrysaetos* in England *Ibis* 129:92–96.
- WYLLIE, I. 1985. Post-fledging period and dispersal of young sparrowhawks *Accipiter nisus*. *Bird Study* 32: 196–198.

Received 4 April 1993; accepted 28 April 1994

HEMATOLOGY AND OCCURRENCE OF HEMOPARASITES IN MIGRATING SHARP-SHINNED HAWKS (*Accipiter striatus*) DURING FALL MIGRATION

LAUREN V. POWERS AND MARK POKRAS

*Tufts Wildlife Clinic, Tufts University School of Veterinary Medicine, 200 Westboro Road,
North Grafton, MA 01536 U.S.A.*

KIM RIO

304 Hellertown St., Hellertown, PA 18055 U.S.A.

CATHY VIVERETTE AND LAURIE GOODRICH

Hawk Mountain Sanctuary, RD 2, Box 191, Kempton, PA 19529 U.S.A.

ABSTRACT.—Packed cell volume (%), total solids (g/dl), white blood cell count (cells/ μ l), differential and absolute white blood cell counts, and prevalence of hemoparasites were determined for 85 healthy sharp-shinned hawks (*Accipiter striatus*) during the 1991 fall migration. The packed cell volume ($47.6 \pm 6.73\%$), total solids (2.83 ± 0.58 g/dl) and white blood cell count ($12\,900 \pm 7310$ cells/ μ l) are within ranges reported previously for other raptors, both captive and wild. Immature birds showed a greater prevalence for the hemoparasites *Hemoproteus* and *Leukocytozoon* than adults but there was no significant difference in prevalence between males and females. These findings add to the small but growing data base on hematology of birds of prey.

KEY WORDS: *hematology; hemoparasites; migration; sharp-shinned hawk; stress.*

Hematología y ocurrencia de hemoparásitos en *Accipiter striatus* migratorios durante la migración otoñal de 1991

RESUMEN.—Se determinó el volumen celular (%), sólidos totales (g/dl), conteo de glóbulos blancos (células/ μ l), conteo diferencial y absoluto de glóbulos blancos y prevalencia de hemoparásitos para 85 individuos saludables de *A. striatus* durante la migración otoñal de 1991. El volumen celular ($47.6 \pm 6.73\%$), los sólidos totales (2.83 ± 0.58 g/dl) y el conteo de glóbulos blancos ($12\,900 \pm 7310$ células/ μ l), están dentro de los rangos reportados previamente para otros rapaces, tanto cautivos como silvestres. Aves inmaduras mostraron una mayor prevalencia de los hemoparásitos *Hemoproteus* y *Leukocytozoon* que los adultos, pero no hubo una diferencia significativa en la prevalencia entre machos y hembras. Estos resultados se agregan a la pequeña pero creciente base de datos sobre la hematología de aves de presa.

[Traducción de Ivan Lazo]

Hematology is a useful tool in determining normal and pathological states in a variety of species including birds. The number of studies on raptor hematology is limited despite the large amount of information available for poultry. In addition, most reports are restricted to captive individuals or birds under rehabilitation and have a small sample size. Previous studies (Hunter and Powers 1980, Gessaman et al. 1986) have examined hematology from free-ranging raptors, which may vary from values obtained from captive birds. The purposes of this study were to add to the data base for hematology of wild raptors and to examine hematologic data for evidence of systemic disease.

MATERIALS AND METHODS

Subjects of our study were migrating sharp-shinned hawks (*Accipiter striatus*) captured for banding purposes at the Little Gap Banding Station near Hawk Mountain Sanctuary in eastern Pennsylvania. Birds were trapped from 9 September to 11 November 1991 between 0630 and 1635 H. Captured birds were weighed to the nearest gram. Each bird was classified as either immature (hatching year) or adult (second year or older) based on plumage characteristics.

Approximately 1 ml blood was collected from the jugular vein. Captured birds were injected with approximately 1 ml lactated Ringer's solution subcutaneously before release. A drop of whole blood was smeared onto a glass slide for measurement of the differential white blood cell count. A sample of whole blood was placed in a mi-

crohematocrit tube (approximately 70 μ l) and spun at 10 000 rpm for 4 min to measure packed cell volume (PCV), or hematocrit. Total solids (TS), an estimate of the protein content, was measured from the plasma using a clinical refractometer.

Samples of whole blood were diluted and stained using a Unopette® Eosinophil staining kit (Becton-Dickinson and Co., Test No. 5877). Stained granulocytes (heterophils, eosinophils and basophils) were counted manually using a hemacytometer. Total white blood cell count (WBC) was calculated using methods described by Dein (1984): cells in 10 squares were counted and the result multiplied by 32 to adjust for dilution. This value was divided by the percentage of staining granulocytes in the differential white blood cell count to adjust for the lack of staining of lymphocytes and monocytes. Blood smears were dipped in the quick stain HEMA-3® (Biochemical Sciences, Inc.) for differential white blood cell counting. One hundred leukocytes were counted and the percent of each cell type was recorded. Differential counts were verified by having each slide read by three different analysts. Absolute white cell counts for each of the types of leukocyte were calculated by multiplying total white blood cell count by the percentage of each cell type in the differential count. Smears were also examined for the presence of blood parasites.

Mean, standard deviation, range, median, and percentiles are reported for the hematologic data. Analysis of variance (ANOVA) and Student *t*-tests were used to detect significant differences in selected parameters. An alpha level of less than 0.05 was considered significant. The Statistical Analysis System (SAS 1988) was used for analysis of data.

RESULTS

Results for packed cell volume (%), total solids (g/dl), white blood cell count (cells/ μ l), relative differential white blood cell count (% cell type), and absolute differential count (cells/ μ l) are presented in Table 1. We found that distributions of PCV, WBC, relative differential counts for heterophils, basophils, and monocytes, and absolute differential counts for all leukocyte types were not statistically normal (Kolmogorov statistic, W: Normal <95%). Therefore, percentiles may be more appropriate for accurate reporting of these data. Comparisons between males and females and between adults and immature birds found no significant differences in hematologic parameters, so results from all birds are compiled in Table 1. Prevalences (% affected) of the blood parasites *Hemoproteus* and *Leukocytozoon* detected from the smears are reported in Table 2. Comparison between males and females found no significant difference for either parasite. Comparison between adults and immature birds found that immature birds had a higher prevalence than adults for both *Hemoproteus* and *Leukocytozoon*. The hemo-

Table 1. Hematology of sharp-shinned hawks captured at Hawk Mountain Sanctuary.

	PCV (%)	TS (g/dl)	WBC (cells/ μ l)	RELATIVE DIFFERENTIAL WBC COUNT (%)					ABSOLUTE DIFFERENTIAL WBC COUNT (cells/ μ l)				
				HET ^a	EO-SIN ^b	BASO ^c	LYMPH ^d	MONO ^e	HET ^a	EOSIN ^b	BASO ^c	LYMPH ^d	MONO ^e
N	85	85	72	81	81	81	81	81	72	72	72	72	72
Mean	47.6	2.83	12 900	27.0	7.67	0.40	63.4	1.60	3200	955	46	8480	187
SD	6.73	0.58	7310	14.2	4.18	0.79	14.4	1.99	2800	715	110	5350	296
Range	30-76	1.4-5.0	2400-37 600	5-69	0-18	0-4	28-90	0-10	240-18 800	0-3380	0-739	1770-23 700	0-1640
Median	47	2.8	11 520	26	7	0	65	1	2470	862	0	7930	111
50% percentile	44-52	2.4-3.2	7680-16 800	16-34	5-11	0-1	54-75	0-3	1810-3630	422-1270	0-22	4030-11 800	0-224
95% percentile	38-56	2.0-3.8	4240-25 400	8-52	1-15	0-2	35-83	0-4	820-9080	80-2520	0-241	1980-17 500	0-744

^a Heterophils.
^b Eosinophils.
^c Basophils.
^d Lymphocytes.
^e Monocytes.

Table 2. Comparison of hemoparasite prevalence between immature and adult sharp-shinned hawks.

	TOTAL (N = 83)	IMMATURE vs. (N = 60)	ADULT (N = 23)	t	df	P
<i>Hemoproteus</i>	20.5%	28.3%	0.00%	2.98	81	0.0038 ^a
<i>Leukocytozoon</i>	16.9%	21.7%	4.35%	2.51	75	0.0143 ^a

^a Student's *t*-test. Probability <0.05 considered significant.

parasite *Plasmodium* was not detected on the blood smears.

Birds with white blood cell counts falling in the second and third quartiles are considered normal for this study. Those with a count above the third quartile are considered leukocytic. Those with a count below the first quartile are termed leukopenic. Comparisons of relative and absolute differential white blood cell counts between normal and leukocytic birds are presented in Table 3. Leukocytic birds had a significant absolute heterophilia, eosinophilia and lymphocytosis. However, differences were not significant between the two groups in relative differential white blood cell counts. Comparisons of relative and absolute differential white blood cell counts between normal and leukopenic birds are presented in Table 4. Leukopenic birds had a significant absolute heteropenia, eosinopenia, and lymphopenia and a significant relative heterophilia.

DISCUSSION

The mean hematocrit value of 47.6% falls within the range of reported values for trapped sharp-

shinned hawks (49.5 ± 2.5%) given by Gessaman et al. (1986) and agrees with previously reported values for other falconiforms (Bond and Gilbert 1958, Elliott et al. 1974, Cooper 1975, Balasch et al. 1976, Smith and Bush 1978, Hunter and Powers 1980, Gee et al. 1981, Ferrer et al. 1987). Hematocrits of migrating, healthy birds of prey may be significantly greater than those in captivity. High altitude is known to increase the production of red blood cells due to the greater demand for efficient oxygen extraction from air. Hemoconcentration from dehydration may occur in migrating birds (Carpenter 1975, Gessaman et al. 1986, Perry et al. 1986) because of relative reduced intake of water. No significant difference was found between the hematocrits of males and females, although it has been suggested that male birds should have a higher hematocrit than females due to the erythropoietic effect of androgens (Gee et al. 1981, Sturkie 1986). Gessaman et al. (1986) found no significant difference in hematocrits between the sexes of trapped sharp-shinned hawks. Hunter and Powers (1980) and Snyder et al. (1980) also found no significant difference between the sexes in either

Table 3. Comparison of differential hematology between sharp-shinned hawks with white blood cell counts above the third quartile (leukocytic) and falling in the second and third quartile (normal).

	TOTAL (N = 81)	LEUKOCYTIC vs. (N = 18)	NORMAL (N = 37)	t	df	P
RELATIVE COUNTS (%)						
Heterophils	27.0	22.1	25.1	0.79	53.0	0.430
Eosinophils	7.67	6.44	8.54	1.82	53.0	0.074
Basophils	0.40	0.28	0.38	0.57	53.0	0.574
Lymphocytes	63.4	69.5	64.4	-1.37	53.0	0.176
Monocytes	1.60	1.61	1.57	-0.07	53.0	0.947
ABSOLUTE COUNTS (cells/ml)						
Heterophils	3200	5270	2880	-2.22	19.1	0.038 ^a
Eosinophils	955	1420	1000	-2.11	53.0	0.039 ^a
Basophils	46	72	43	-0.66	20.0	0.518
Lymphocytes	8480	15 400	7720	-6.88	24.4	0.0001 ^a
Monocytes	187	321	163	-1.29	19.8	0.21

^a Student's *t*-test. Probability <0.05 considered significant.

Table 4. Comparison of differential hematology between sharp-shinned hawks with white blood cell counts below the third quartile (leukopenic) and falling in the second and third quartile (normal).

	TOTAL	LEUKOPENIC	vs.	NORMAL	<i>t</i>	df	<i>P</i>
RELATIVE COUNTS (%)	(<i>N</i> = 81)	(<i>N</i> = 26)		(<i>N</i> = 37)			
Heterophils	27.0	33.0		25.1	-2.27	61.0	0.027 ^a
Eosinophils	7.67	7.27		8.54	1.13	61.0	0.263
Basophils	0.40	0.50		0.38	-0.52	37.5	0.607
Lymphocytes	63.4	57.8		64.4	1.90	61.0	0.063
Monocytes	1.60	1.65		1.57	-0.20	60.7	0.842
ABSOLUTE COUNTS (cells/ml)	(<i>N</i> = 72)	(<i>N</i> = 17)		(<i>N</i> = 37)			
Heterophils	3200	1720		2880	-3.39	48.7	0.001 ^a
Eosinophils	955	361		1000	-5.24	51.9	0.0001 ^a
Basophils	46	26		43	-0.75	52.0	0.454
Lymphocytes	8480	2840		7720	-9.88	46.7	0.0001 ^a
Monocytes	187	98		163	-1.72	50.1	0.091

^a Student's *t*-test. Probability <0.05 considered significant.

trapped or captive American kestrels (*Falco sparverius*). Age may also have an effect on hematocrit in that immature birds should have higher hematocrit values than adults (Rehder et al. 1982). No significant difference was found between immature birds and adults for hematocrit values in this study or that by Gessaman et al. (1986).

The mean total solids value of 2.83 g/dl was less than that reported previously for some falconiforms (Elliott et al. 1974, Halliwell et al. 1975, Smith and Bush 1978, Gee et al. 1981, Ferrer et al. 1987) but within the range reported by Balasch et al. (1976) and Snyder et al. (1980). Accurate comparisons with previously reported results may not be possible due to the different techniques in measuring protein levels in blood such as the Biuret and refractometric methods. Lumeij and de Bruijne (1985) showed that total solids measured with a refractometer have little correlation with serum protein levels measured by the Biuret method in rock doves (*Columba livia*). A low total solids value is often indicative of poor nutrition in raptors (Smith and Bush 1978, Ferrer et al. 1987). No significant difference in total solids was found between males and females or between adults and immature birds. These findings agree with those reported previously for some falconiforms (Snyder et al. 1980).

The prevalence of *Hemoproteus* in immature sharp-shinned hawks was 28.3%, yet no adults showed *Hemoproteus* parasitemia on the blood smears. On a similar note, 21.7% of immature birds had *Leukocytozoon* but only 4.35% of adults showed signs of

infection. No significant difference in hemoparasite prevalence was found between males and females. This finding is in agreement with previous reports (Kirkpatrick and Suthers 1988, Davidar and Morton 1993). The greater prevalence of *Hemoproteus* and *Leukocytozoon* in immature sharp-shinned hawks from this study is in contrast to other reports. Kirkpatrick and Suthers (1988) found that hatching-year birds were infected at a lower rate than older birds representing 59 species from central New Jersey. Yearling purple martins (*Progne subis*) were significantly less infected with *Hemoproteus prognei* than adults (Davidar and Morton 1993). Ashford et al. (1990) reported a higher prevalence of *Leukocytozoon toddi* in adult sparrowhawks (*Accipiter nisus*). This study also suggested a vertical mode of transmission from adults to young in the nest through vector species (*Culicoides* for *Hemoproteus* and ornithophilic members of the family Simuliidae for *Leukocytozoon*). Relapses of hemoparasitemia as birds become stressed or begin breeding has been suggested (Peirce 1980). A loss of detectable levels of hemoparasite in the peripheral blood (latency) between the months of October and April with a spring relapse was reported by Ashford et al. (1990). It is not unreasonable to suggest that immature sharp-shinned hawks become infected in the nest and are less able to achieve latency of infection with hemoparasites due to their naive immunologic status and because of the stresses of first migration and incompletely developed hunting skills. The clinical effects of hemoparasites have not been completely deter-

Table 5. Total and relative differential white blood cell counts reported in various raptors.

	N	RELATIVE DIFFERENTIAL WBC COUNT (%)					AUTHOR
		WBC (cells/ $\mu\text{l} \times 10^3$)	HETEROPHILS	EOSINOPHILS	BASOPHILS	LYMPHOCYTES	
Common buzzard (<i>Buteo buteo</i>)	11	14.0-49.0	20.5-39.8	5.5-19	0.25-8	35-65.5	0.25-3.75 a
Honey buzzard (<i>Pernis apivorus</i>)	1	10.5	29.8	9	4.8	55.3	1.25 a
Andean condor (<i>Vultur gryphus</i>)	1	13.5	42.8	11	2.5	42	1.8 a
Golden eagle (<i>Aquila chrysaetos</i>)	1	23.5	52.5	6	3.3	34	4.3 a
White-tailed sea eagle (<i>Haliaeetus albicilla</i>)	1	19.5	32.3	9.5	1.3	55	2 a
Imperial eagle (<i>Aquila heliaca</i>)	1	15.0	44	11.8	2.3	40.3	1.3 a
Tawny eagle (<i>Aquila rapax</i>)	1	42.5	57.3	10	2	30	0.8 a
Marsh harrier (<i>Circus aeruginosus</i>)	3	9.0-33.0	26.5-39.5	1.5-6.5	2.8-5.3	48-59.5	2.5-10.5 a
Common kestrel (<i>Falco tinnunculus</i>)	5	14.5-57.0	11.3-33	8.75-59.3	1.5-3.8	24-57.5	0.25-3.0 a
Black kite (<i>Milvus migrans</i>)	5	10.0-28.0	28.8-35.3	12.8-35.5	2.3-3.5	29.5-50.5	0-2 a
Red kite (<i>Milvus milvus</i>)	1	12.0	19.5	28.3	2.8	48.8	0.75 a
Egyptian vulture (<i>Neophron percnopterus</i>)	1	29.5	43.8	5.5	8.5	37.5	4.8 a

Table 5. Continued.

	N	RELATIVE DIFFERENTIAL WBC COUNT (%)				MONOCYTES	AUTHOR
		WBC (cells/ μl × 10 ³)	HETEROPHILS	EOSINOPHILS	BASOPHILS	LYMPHOCYTES	
King vulture (<i>Sarcoramphus papa</i>)	2	41.9					b
Hooded vulture (<i>Necrosyrtes monachus</i>)	1	22.4					b
Savannah hawk (<i>Heterospizias meridionalis</i>)	1	31.0					b
Ornate hawk-eagle (<i>Spizaetus ornatus</i>)	1	33.0					b
White-bellied sea eagle (<i>Haliaeetus leucogaster</i>)	1	22.0					b
Crested serpent eagle (<i>Spilornis cheela</i>)	1	22.0					b
Bald eagle (<i>Haliaeetus leucocephalus</i>)	1	11.3					b
Collared forest falcon (<i>Microstur semitorquatus</i>)	1	26.4					b
Crested caracara (<i>Polyborus plancus</i>)	2	24.1					b
Red-tailed hawk (<i>Buteo jamaicensis</i>)	2	6-46					c
Harris' hawk (<i>Parabuteo unicinctus</i>)	2	12-14					c

^a Christoph and Borowski (1961).
^b Elliott et al. (1974).
^c Halliwell et al. (1975).

mined. Hemoparasites have been shown to increase rehabilitation time in raptors (Olsen and Gaunt 1985). However, most studies on wild birds show no evidence of decreased longevity or reproductive ability in infected birds (Kirkpatrick and Suthers 1988, Ashford et al. 1990, Davidar and Morton 1993), although a negative effect on mate selection has been suggested (Kirkpatrick and Suthers 1988, Ashford et al. 1990, Davidar and Morton 1993). No significant differences in measured hematologic parameters were identified between hemoparasitemic and non-hemoparasitemic birds in our study, indicating no correlation between infection and other hemogram indicators of general health status.

The mean total WBC was $12\,900 \pm 7310$ cells/ μ l. This value falls within range of normal counts for other falconiforms (Elliott et al. 1974, Halliwell et al. 1975, Smith and Bush 1978). The relative differential white cell counts also agree with those previously reported (Table 5). It is difficult, if not impossible, to measure normal white blood cell counts accurately in raptors since these birds are unavoidably stressed when handled and especially when captured in the wild. Migration is also a source of stress to a raptor. ACTH and corticosteroids have been shown to be elevated during periods of stress in birds (Wolford and Ringer 1962). In poultry the hematologic response to corticosteroids is leukocytosis with heterophilia and lymphopenia (Hublé 1955, Glick 1961, Bell and Freeman 1971). However, it must be emphasized that the hematologic response to stress varies from species to species. For example, Bhattacharyya and Sarkar (1968) found that in the rock dove, the house crow (*Corvus splendens*) and the cattle egret (*Bubulcus ibis*) the response to cortical stimulation by ACTH and unilateral adrenalectomy was heteropenia and lymphocytosis. Only the common myna (*Acridotheres tristis*) responded in a similar fashion to poultry with heterophilia and lymphopenia in that study.

Levels of epinephrine and norepinephrine have been shown to be elevated during migration of the common snipe (*Gallinago gallinago*) and the rose-colored starling (*Sturnus roseus*; Epple and Stetson 1980). Information about the effect of catecholamines on avian hematology is lacking, but these substances are known to cause leukocytosis with neutrophilia and lymphocytosis in mammals (Duncan and Prasse 1986). Without having measured serum levels of catecholamines and corticosteroids during this study, it is impossible to determine the relative

level of stress for each bird. Birds with a total white blood cell count above the third quartile (leukocytic) had an absolute heterophilia, lymphocytosis and eosinophilia which may reflect more of a catecholamine-induced stress pattern rather than a corticosteroid-induced hemogram (which should present with lymphopenia). However, we caution against over-interpretation of the data since hormone levels were not measured and the effects of catecholamines and glucocorticoids on the hemogram are not known. Leukocytosis is often present with bacterial, fungal or parasitic infections, whereas leukopenia may accompany viral infections. Most hawks captured in this study appeared healthy on physical examination, showing no signs of clinical disease. Seriously ill birds might not be able to migrate and therefore would not be included in this study. Birds in this study with leukocytosis or leukopenia may have been ill, but the source of possible infection was not determined. We warn, however, that with lure traps a hungrier subset of the migrating population might have been sampled. This group may include birds who have no evidence of disease yet are subclinically ill and perhaps hungrier than healthy birds. But because no evidence of clinically significant disease states could be detected in the subjects, the white blood cell counts and other hematologic parameters for all birds from this study should be analyzed as a spectrum of hematologic findings for migrating, clinically healthy sharp-shinned hawks.

ACKNOWLEDGMENTS

The authors wish to thank the Wharton Trust, the Bailey Wildlife Foundation and the Hawk Migration Association of North America for providing support for this study. We thank Jerry Lehr and all the staff of the Little Gap Banding Station for assisting in this study. The Tufts Wildlife Clinic and its director, Charles J. Sedgwick, generously provided space and resources for laboratory and data analyses. Carolyn Haseltine lent her considerable expertise in avian hematology to the training of project personnel and interpretation of slides. This is Hawk Mountain Contribution number 21.

LITERATURE CITED

- ASHFORD, R.W., I. WYLLIE AND I. NEWTON. 1990. *Leukocytozoon toddi* in British sparrowhawks *Accipiter nisus*: observations on the dynamics of infection. *J. Nat. Hist.* 24:1101-1107.
- BALASCH, J., S. MUSQUERA, L. PALACIOS, M. JIMENEZ AND J. PALOMEQUE. 1976. Comparative hematology of some falconiforms. *Condor* 78:258-259.
- BELL, D.J. AND B.M. FREEMAN. 1971. Physiology and

- biochemistry of the domestic fowl. Academic Press, New York, NY U.S.A.
- BHATTACHARYYA, T.K. AND A.K. SARKAR. 1968. Avian leukocytic responses induced by stress & corticoid inhibitors. *Indian J. Exp. Biol.* 6:26-28.
- BOND, C.F. AND P.W. GILBERT. 1958. Comparative study of blood volume in representative aquatic and nonaquatic birds. *Am. J. Physiol.* 194:519-521.
- CARPENTER, F.L. 1975. Bird hematocrits: effects of high altitude and strength of flight. *Comp. Biochem. Physiol.* 50A:415-417.
- CHRISTOPH, H.J. AND G. BOROWSKI. 1961. Beiträge zur Hämatologie der Zootiere. IV. Das Blutbild von Greifvögeln (Accipitres) unter besonderer Berücksichtigung einiger in Deutschland noch heimischer kleinerer Arten. *Kleintier-Praxis* 6:71-76.
- COOPER, J.E. 1975. Haematological investigations in East African birds of prey. *J. Wildl. Dis.* 11:389-394.
- DAVIDAR, P. AND E.S. MORTON. 1993. Living with parasites: prevalence of a blood parasite and its effect on survivorship in the purple martin. *Auk*. 110:109-116.
- DEIN, F.J. 1984. Laboratory manual of avian hematology. Association of Avian Veterinarians, Boca Raton, FL U.S.A.
- DUNCAN, J.R. AND K.W. PRASSE. 1986. Veterinary laboratory medicine. Iowa State Univ. Press, Ames, IA U.S.A.
- ELLIOTT, R.H., E.E. SMITH AND M. BUSH. 1974. Preliminary report on hematology of birds of prey. *J. Zoo Anim. Med.* 5:11-16.
- EPPLÉ, A. AND M.H. STETSON. 1980. Avian endocrinology. Academic Press, New York, NY U.S.A.
- FERRER, M., T. GARCÍA-RODRÍGUEZ, J.C. CARRILLO AND J. CASTROVIEJO. 1987. Hematocrit and blood chemistry in captive raptors (*Gyps fulvus*, *Buteo buteo*, *Milvus migrans*, *Aquila heliaca*). *Comp. Biochem. Physiol.* 87A: 1123-1127.
- GEE, G.F., J.W. CARPENTER AND G.L. HENSLER. 1981. Species differences in hematological values of captive cranes, geese, raptors, and quail. *J. Wildl. Manage.* 45: 463-483.
- GESSAMAN, J.A., J.A. JOHNSON AND S.W. HOFFMAN. 1986. Hematocrits and erythrocyte numbers for Cooper's and sharp-shinned hawks. *Condor* 88:95-96.
- GLICK, B. 1961. The effect of bovine growth hormone, desoxycorticosterone acetate, and cortisone acetate on the white blood cell counts of 2-week-old chickens. *Poult. Sci.* 40:1537-1539.
- HALLIWELL, W.H., G. IVINS, D.A. SCHMIDT AND G. WEDDLE. 1975. A preliminary report on the hematology and chemical profiles in selected birds of prey. *Proc. Ann. Meet. Am. Assoc. Zoo Vet.* 188-196.
- HUBLÉ, J. 1955. Haematological changes in cockerels after ACTH and cortisone-acetate treatment. *Poult. Sci.* 34:1357-1359.
- HUNTER, S.R. AND L.R. POWERS. 1980. Raptor hematocrit values. *Condor* 82:226-227.
- KIRKPATRICK, C.E. AND H.B. SUTHERS. 1988. Epizootiology of blood parasite infections in passerine birds from central New Jersey. *Can. J. Zool.* 66:2374-2382.
- LUMEIJ, J.T. AND J.J. DE BRUIJNE. 1985. Evaluation of the refractometric method for the determination of total protein in avian plasma or serum. *Avian Path.* 14 441-444.
- OLSEN, G.H. AND S.D. GAUNT. 1985. Effect of hemoprotozoal infections on rehabilitation of wild raptors. *J. Am. Vet. Med. Assoc.* 187:1204-1205.
- PEIRCE, M.A. 1980. Current knowledge of the haematozoa of raptors. Pages 15-19 in J.E. Cooper and A.G. Greenwood [EDS.], Recent advances in the study of raptor diseases. Chiron Publications Ltd., West Yorkshire, U.K.
- PERRY, M.C., H.H. OBRECHT, B.K. WILLIAMS AND W.J. KUENZEL. 1986. Blood chemistry and hematocrit of captive and wild canvasbacks. *J. Wildl. Manage.* 50 435-441.
- REHDER, N.B., D.M. BIRD, P.C. LAGUË AND C. MACKAY. 1982. Variation in selected hematological parameters of captive red-tailed hawks. *J. Wildl. Dis.* 18:105-109.
- SAS INSTITUTE, INC. 1988. SAS/STAT user's guide. Statistics. SAS Inst., Inc., Cary, NC U.S.A.
- SMITH, E.E. AND M. BUSH. 1978. Haematologic parameters on various species of Strigiformes and Falconiformes. *J. Wildl. Dis.* 14:447-450.
- SNYDER, J.E., D.M. BIRD AND P.C. LAGUË. 1980. Variations in selected parameters in the blood of captive American kestrels. Pages 113-115 in J.E. Cooper and A.G. Greenwood [EDS.], Recent advances in the study of raptor diseases. Chiron Publications Ltd., West Yorkshire, U.K.
- STURKIE, P.D. 1986. Body fluids: blood. Page 112 in P.D. Sturkie [ED.], Avian physiology. Springer-Verlag, New York, NY, U.S.A.
- WOLFORD, J.H. AND R.K. RINGER. 1962. Adrenal weight, adrenal ascorbic acid, adrenal cholesterol and differential leucocyte counts as physiological indicators of "stressor" agents in laying hens. *Poult. Sci.* 41:1521-1529.

Received 3 May 1993; accepted 7 May 1994

A RAPTOR ROADSIDE SURVEY IN WESTERN TURKEY AND EASTERN GREECE

WADE L. EAKLE¹

World Working Group on Birds of Prey and Owls, Wangenheimstr. 32, D-1000 Berlin 33, Germany

ABSTRACT.—Roadside surveys were conducted in western Turkey and eastern Greece in April–May 1993 to determine the relative abundance of observed raptors. Ten diurnal species, as well as unidentified buzzards and unidentified harriers, and one nocturnal species were observed during 177 hr 30 min of observation over 4395 km travelled. Lesser kestrels (*Falco naumanni*), common kestrels (*F. tinnunculus*), common buzzards (*Buteo* spp.) and harriers (*Circus* spp.) were the most frequently observed species. More individuals ($N = 145$) and species ($N = 8$) were observed in agricultural lands than other habitat types. Indices of relative abundance were calculated for each species based on the number of individuals observed per kilometer travelled.

KEY WORDS: *Greece; raptor roadside survey; relative abundance; Turkey.*

Observación de rapaces en rutas del oeste de Turquía y el este de Grecia

RESUMEN.—Un estudio de ruta fue hecho en el oeste de Turquía y en el este de Grecia entre abril y mayo de 1993, para determinar la abundancia relativa de rapaces observados. Se observaron diez especies diurnas, incluyendo *Buteo* spp. y *Circus* spp. no identificados, y una especie nocturna, en un recorrido de 4395 km realizado en 177 hr 30 min. *Falco naumanni*, *F. tinnunculus*, *Buteo* spp. y *Circus* spp. fueron las especies observadas con mayor frecuencia. Se observaron más individuos ($N = 145$) y especies ($N = 8$) en tierras de uso agrícola que en otros tipos de hábitat. Se calcularon índices relativos para cada especie basados en el número de individuos observados por kilómetro recorrido.

[Traducción de Ivan Lazo]

Raptor population densities in Turkey and Greece, particularly Turkey, are poorly documented. Belkis et al. (1977) and Beaman and Porter (1985) summarized the status of 37 diurnal raptors known to winter or breed in Turkey. Vagliano (1977) reported on the status of 36 diurnal species in Greece and summarized their occurrence by habitat types. Cosson (1985) recorded six diurnal and two nocturnal species breeding on Rhodes and estimated relative abundance indices for the long-legged buzzard (*Buteo rufinus*). Additionally, the number of breeding pairs and population trends for the four vultures in Greece were estimated by Handrinos (1985), while Vagliano (1985) reported on little owl (*Athene noctua*) populations on Crete. Hallmann (1985) reported that 26 diurnal species breed in Greece, but provided no discussion of methods used to derive this population estimate. Handrinos and Demetropoulos (1983) estimated breeding pairs of 36 diurnal and

eight nocturnal species in Greece, and Gensbol (1987) for 27 diurnal species in Greece and 28 diurnal species in Turkey, but again, no discussion of methods used to develop these population estimates were provided by the authors.

Relative abundance estimates have been widely used in raptor inventories and monitoring studies for investigating population dynamics, monitoring status, and evaluating responses to changes in the environment (Fuller and Mosher 1987). Relative abundance generally refers to the contribution a species makes to the total abundance of that wildlife community (Jones 1986). There are several ways to estimate relative abundance, including the number of raptors seen per hr of observation or per linear distance, and the number of owl calls heard per hr (Kochert 1986). In this study I used numbers of individuals observed per kilometer travelled for a roadside survey of raptors in western Turkey and eastern Greece. These results represent perhaps the first and most comprehensively reported indices of observed relative abundance collected by such method for raptor populations in this part of the world.

¹ Present address: U.S. Army Corps of Engineers, San Francisco District, Regulatory Branch, 211 Main Street, San Francisco, CA 94105–1905 U.S.A.



Figure 1. Raptor survey route in western Turkey and eastern Greece, including the islands of Rhodes and Crete, 9 April to 13 May 1993.

STUDY AREA AND METHODS

Western Turkey, which is part of Asia Minor, includes eastern Thrace from the city of Edirne to Istanbul, the peninsula of Gallipoli, the Sea of Marmara, the coastal region of the Aegean Sea, and central Anatolia including the region of Capadocia. On the southern shore of the Sea of Marmara are low hills used for grazing, farming and industry, and higher pine-forested mountains, such as Uludag (Mt. Olympus) near Bursa which reaches 2583 m (Fig. 1). The mean annual rainfall in this region is approximately 670 mm. The Aegean Sea coast is a region of plains and river valleys. Olive, fig and fruit orchards can be seen on hillsides, and tobacco and sunflower fields in valleys. Central Anatolia which embraces Capadocia is a vast plateau (rolling steppe) with a mean elevation of 1000 m where sheep grazing and wheat growing are primary land uses. The plateau is surrounded by mountain ranges with elevations to 2500 m, some being volcanoes with snow-capped peaks (Dubin and Lucas 1989, Brosnahan 1990).

In the month of March, the mean daily minimum and maximum temperatures in Istanbul are 3–30°C, in Ankara 0–11°C, in Bursa 4–13°C, and in Izmir (on the Aegean Sea coast) 6–16°C. In May, these temperatures are 12–

21°C in Istanbul, 9–22°C in Ankara, 11–23°C in Bursa, and 14–26°C in Izmir (Brosnahan 1990).

Eastern Greece, the southernmost of the Balkan states, includes the Peloponnese from the Mani to Corinthia and Argolis (including Laconia and Arcadia), Thessaly, Macedonia, and western Thrace. Roadside counts on the island of Crete included the region near Iraklio to Kastelli on the western end of the island. Landscapes and land uses similar to those observed in Turkey were found on mainland Greece and Crete. These included mountains in the Mani peninsula, plains and mountains (Mt. Olympus, 2917 m) in Thessaly, black pine (*Pinus nigra*) forests in Macedonia, and the Evros River valley and Porto-Lagos wetlands in Thrace (Fig. 1).

On Crete, largest of the Greek islands, climatic and geographic conditions are similar to North Africa, although mountains such as Mt. Ida (2456 m), are snow-capped for several months of the year (Handrinos and Demetropoulos 1983). Lower mountain slopes and hills support low phrygana or maquis vegetation, Kermes oak (*Quercus coccifera*), locust (*Ceratonia siliqua*), and juniper (*Juniperus* spp.; Handrinos 1985; Fig. 1).

My study area is classified as two biomes. The region around the Aegean Sea included Crete, the Sea of Marmara, and Gallipoli was classified as evergreen sclero-

Table 1. Survey routes, mode of travel, and distance travelled for raptor surveys conducted in Turkey and Greece, April–May 1993.

DATE	SURVEY ROUTE	TIME OF DAY	MODE OF TRANSPORTATION	DISTANCE (km)
9 April	Istanbul–Ankara	1030–1800	train	450
10 April	Nevsehir–Derinkuyu	0900–1600	bus/foot	60
11 April	Nevsehir–Goreme	1030–2000	bus/foot	20
12 April	Goreme–Cavusin–Zelve	0900–1730	foot	15
13 April	Goreme–Bursa	0700–1800	bus	695
14 April	Bursa–Uludag	0900–1700	car/foot	65
15 April	Bursa–Canakkale	1000–1430	bus	310
16 April	Gallipoli	1000–1600	bus/foot	50
17 April	Troy–Canakkale–Bergama	1000–2000	bus/foot	300
18 April	Bergama (Pergamum)	1000–1700	foot	10
19 April	Bergama–Selcuk	1200–1530	bus	180
20 April	Selcuk (Ephesus)	0800–1600	foot	15
21 April	Selcuk–Bodrum	1200–1500	bus	170
22 April	Bodrum	1000–1600	foot	5
23 April	Bodrum–Marmaris	1000–1330	bus	165
26 April	Iraklio–Knossos	1000–1600	bus/foot	15
27 April	Iraklio–Kalimaki	1130–1630	bus/foot	65
28 April	Kalimaki–Hania	0800–1700	bus/foot	150
29 April	Hania–Samaria–Kastelli	0730–2130	bus/foot	170
1 May	Gythio–Caves of Diros	1000–1400	bus	70
2 May	Gythio–Naphlio	0830–1630	bus	180
3 May	Naphlio–Myceane	1000–1400	bus	65
4 May	Naphlio	1030–1830	foot	10
5 May	Naphlio–Athens	1000–1430	bus	145
10 May	Athens–Thessaloniki	0700–1330	train	530
12 May	Thessaloniki–Komotini	1400–2030	train	415
13 May	Kabacka–Istanbul	0630–0730	train	70
Total distance				4395
Total observation time		177 hr 30 min		

phyllus forests, scrub or woodlands, and central Anatolia as cold winter (continental) desert and/or semi-desert (UNESCO 1987).

Roadside counts were conducted primarily by means of public bus, but some routes were surveyed by train, car, and on foot. All means of transportation provided excellent viewing opportunities, allowing two observers to focus on locating and identifying raptors on both sides of the road or railroad track. Unfortunately, driving speeds were variable and not always known, nor was it possible to stop the vehicle to identify distant birds or estimate the distance of the raptor from the survey vehicle. Visibility was comparable for buses and trains. Data recorded for each observation included date, time, location, species, age and sex (if possible), number, habitat type, activity, and perching substrate.

Surveys were conducted in western (Asian) Turkey from 9–23 April 1993, and in eastern Greece, including Crete, from 26 April to 12 May 1993. Additional data were collected in northwestern (European) Turkey (eastern

Thrace) on 13 May 1993. Survey times ranged from 0630–2130 H. Weather conditions were variable during the survey period, but mostly without any precipitation.

I used the method developed by Woffinden and Murphy (1977) to calculate an index of observed relative abundance for each raptor species sighted:

$$\text{Index} = \frac{\text{Total number of a species observed}}{\text{Total kilometers travelled}} \times 1000$$

RESULTS AND DISCUSSION

Nearly 4400 km were travelled and approximately 177 hr of observation time logged (Table 1), yielding 1.05 individual raptors sighted per hour of observation time, or 23.7 km travelled per bird sighted (0.04 individual raptors sighted per kilometer).

Lesser kestrels (*Falco naumanni*) and common kestrels (*F. tinnunculus*) were the most commonly

observed raptor species, followed by unidentified *Buteo* species, long-legged buzzards, and unidentified *Circus* species (Table 2). Lesser and common kestrels accounted for 71% of individual raptors sighted, followed by *Buteo* species (16%; Table 2). The unidentified buteos ($N = 20$) were most likely long-legged buzzards and common buzzards (*B. buteo*) given the time of year and location of the survey route (Gensbol 1987 and C.G. Vlachos pers. commun.).

Most of the species observed are migratory over a portion of their range, but some are year-round residents in Turkey and Greece. During March through May, many of these species could be migrating through the region to more northern breeding grounds or returning to local nesting areas (Gensbol 1987). Species thought to be year-round residents in the region include the griffon vulture (*Gyps fulvus*), sparrowhawk (*Accipiter nisus*), and common and long-legged buzzards. Both harrier species (western marsh harrier [*C. aeruginosus*], and Montagu's harrier [*C. pygargus*]) that breed in Turkey and Greece generally return to nesting areas in April (Gensbol 1987). Three of the four falcons observed are long distance migrants and summer throughout Greece and Turkey. The lesser kestrel is often seen in small flocks on spring migration (Gensbol 1987), and in fact, 10 flocks of kestrels with as many as 19 individuals were observed during the survey. The common kestrel is a year-round resident.

Lesser and common kestrels accounted for over 75% of the raptors sighted in agricultural lands (Table 3). Agricultural lands supported the greatest number of species (61%) and individuals observed (78%). Harriers, long-legged buzzards, unidentified *Buteo* species, lesser kestrels, and common kestrels were sighted more frequently in agricultural lands than all other habitat types encountered (Table 3). Unidentified *Buteo* species were observed in six habitat types, while all other species were observed in three or fewer habitat types.

Road transects are often used to obtain indices to raptor abundance or density in order to assess or compare population structure, seasonal population changes, habitat use, distribution, yearly population trends, and to determine activity (Millsap and LeFranc 1988). However, road counts are affected by a number of biases. Perhaps the most significant inherent bias associated with road counts is species detectability, or the detectable distance of a raptor,

Table 2. Frequency of sightings and observed relative abundance indices of raptors sighted during surveys in Turkey and Greece, April–May 1993.

SPECIES	NUM- BER OB- SERVED	KM TRAVELLED PER IN- DIVIDUAL	INDEX OF REL- ATIVE ABUN- DANCE ^a
Lesser kestrel (<i>Falco naumanni</i>)	75	58.6	17.1
Common kestrel (<i>Falco tinnunculus</i>)	57	77.1	13.0
<i>Buteo</i> spp.	20	219.7	4.5
Long-legged buzzard (<i>Buteo rufinus</i>)	10	439.5	2.3
<i>Circus</i> spp.	9	488.3	2.1
Eleonora's falcon (<i>Falco eleonora</i>)	3	1465.0	0.7
Common buzzard (<i>Buteo buteo</i>)	3	1465.0	0.7
Black kite (<i>Milvus migrans</i>)	2	2197.5	0.5
European hobby (<i>Falco subbuteo</i>)	2	2197.5	0.5
Griffon vulture (<i>Gyps fulvus</i>)	1	4395.0	0.2
Sparrowhawk (<i>Accipiter nisus</i>)	1	4395.0	0.2
Booted eagle (<i>Hieraaetus pennatus</i>)	1	4395.0	0.2
Little owl (<i>Athene noctua</i>)	1	4395.0	0.2

^a Analysis of relative abundance after Woffinden and Murphy (1977)

which can vary by species, activity, habitat, and behavior (Fuller and Mosher 1987). Millsap and LeFranc (1988) believed several assumptions are violated in many raptor road transect studies, and suggested presenting results based on volume of habitat searched for more direct comparison of results between studies. However, their method requires additional time to measure vegetation variables necessary to calculate volume estimates. Kochert (1986) recommended recording all birds seen on road counts used as line transects, and measuring their perpendicular distances from the transect centerline regardless of their distance and analyzing these data with a line transect computer program.

The problem of species detectability was encountered during the roadside surveys in Turkey and Greece. Habitat types that provided the highest spe-

Table 3. Numbers of raptors observed in habitat types in Turkey and Greece, April–May 1993.

SPECIES	HABITAT TYPES ^a								
	W	A	F	S	U	C	O	R	L
Black kite	—	—	1	—	—	1	—	—	—
Griffon vulture	—	—	1	—	—	—	—	—	—
<i>Circus</i> spp.	1	8	—	—	—	—	—	—	—
Sparrowhawk	—	—	—	—	—	1	—	—	—
Common buzzard	—	1	—	—	—	—	—	1	1
Long-legged buzzard	—	9	—	—	—	1	—	—	—
<i>Buteo</i> spp.	1	14	1	1	1	2	—	—	—
Booted eagle	—	1	—	—	—	—	—	—	—
Lesser kestrel	—	57	—	—	15	3	—	—	—
Common kestrel	—	53	—	—	1	—	3	—	—
Eleonora's falcon	—	—	—	—	—	—	3	—	—
European hobby	—	2	—	—	—	—	—	—	—
Little owl	—	—	—	—	—	1	—	—	—
Total species	2	8	3	1	3	6	2	1	1
Total individuals	2	145	3	1	17	9	6	1	1

^a Habitat types (W = wetland, A = agricultural land, F = pine forest, S = steppe, U = urban, C = chaparral/scrub-shrub, O = ocean/coast, R = riparian/riverine, L = lake shore).

cies detectability clearly included the vast, open agricultural lands of central Anatolia, Thessaly, Macedonia, and Thrace, as well as some urban areas near Ankara, Bursa, and Thessaloniki, and along the coast of the Aegean Sea. Species detectability was lowest in habitat types with greater plant species and structural diversity (e.g., black pine forest and riparian areas). Accordingly, species such as kestrels and buzzards that were more likely to be observed in open habitats were recorded in greater numbers. Substrates for perching, such as power and telephone poles, were also typically located along roads and railroad tracks.

ACKNOWLEDGMENTS

A. Baycin and C.G. Vlachos provided logistical support in Istanbul, Turkey and Thessaloniki, Greece, respectively. L.A. Barekman assisted in the field. P.J. Scheetz prepared the figure of Turkey and Greece. M.R. Jennings, R.W. Mannan, T.G. Grubb, D. Ledig, D.K. Garcelon, A. Fish, and C.G. Vlachos provided critical comments on a first draft of the manuscript. The manuscript was improved by reviews by B.A. Millsap and two anonymous reviewers. B.-U. Meyburg provided study endorsement from the World Working Group on Birds of Prey and Owls (International Council for Bird Preservation [ICBP] and Species Survival Commission [SSC] of the International Union for the Conservation of Nature and Natural Resources [IUCN]).

LITERATURE CITED

BEAMAN, M. AND R.F. PORTER. 1985. Status of birds of prey in Turkey. Pages 52–56 in R.D. Chancellor and B.-U. Meyburg [EDS.], Bull. No. 2 of the World Working Group on Birds of Prey. Berlin, Germany and Paris, France.

BELKIS, A., M. BEAMAN AND R.F. PORTER. 1977. Status and migration of birds of prey in Turkey. Pages 182–187 in R.D. Chancellor [ED.], World conference on birds of prey, Report of Proceedings, International Council for Bird Preservation. Hampshire, U.K.

BROSNAHAN, T. 1990. Turkey—a travel survival kit. Lonely Planet Publ. Berkeley, CA U.S.A.

COSSON, F. 1985. Some recent data of the raptors of Rhodes (Greece). Pages 57–60 in R.D. Chancellor and B.-U. Meyburg [EDS.], Bull. No. 2 of the World Working Group on Birds of Prey. Berlin, Germany and Paris, France.

DUBIN, M. AND E. LUCAS. 1989. Trekking in Turkey. Lonely Planet Publ. Berkeley, CA U.S.A.

FULLER, M.R. AND J.A. MOSHER. 1987. Raptor survey techniques. Pages 37–65 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline and D.M. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC U.S.A.

GENSBOL, B. 1987. Collins guide to the birds of prey of Britain and Europe, North Africa and the Middle East. Collins, London, U.K.

HALLMANN, B. 1985. Status and conservation problems of birds of prey in Greece. Pages 55–59 in I. Newton

- and R.D. Chancellor [EDS.], Conservation studies on raptors. International Council for Bird Preservation Tech. Publ. No. 5. Cambridge, U.K.
- HANDRINOS, G. 1985. The status of vultures in Greece. Pages 103–115 in I. Newton and R.D. Chancellor [EDS.], Conservation studies on raptors. International Council for Bird Preservation Tech. Publ. No. 5. Cambridge, U.K.
- AND A. DEMETROPOULOS. 1983. Birds of prey of Greece. Efstathiadis Group. Athens, Greece.
- JONES, K.B. 1986. Data types. Pages 11–28 in A.Y. Cooperrider, R.J. Boyd and H.R. Stuart [EDS.], Inventory and monitoring of wildlife habitat. U.S. Bur. Land Manage. Denver, CO U.S.A.
- KOCHERT, M.N. 1986. Raptors. Pages 313–349 in A.Y. Cooperrider, R.J. Boyd and H.R. Stuart [EDS.], Inventory and monitoring of wildlife habitat. U.S. Bur. Land Manage. Denver, CO U.S.A.
- MILLSAP, B.A. AND M.N. LEFRANC, JR. 1988. Road transect counts for raptors: how reliable are they? *J Raptor Res.* 22:8–16.
- UNESCO. 1987. Man and the biosphere program. Map of biosphere reserves and biome classification.
- VAGLIANO, C. 1977. The status of birds of prey in Greece. Pages 118–125 in R.D. Chancellor [ED.], World conference on birds of prey, Report of Proceedings, International Council for Bird Preservation. Hampshire, U.K.
- . 1985. The little owl *Athene noctua* in Crete (Greece). Pages 107–108 in R.D. Chancellor and B.-U. Meyburg [EDS.], Bull. No. 2 of the World Working Group on Birds of Prey. Berlin, Germany and Paris, France.
- WOFFINDEN, N.D. AND J.R. MURPHY. 1977. A roadside raptor census in the eastern Great Basin—1973–1974. *Raptor Res.* 11:62–66.

Received 14 January 1994; accepted 6 May 1994.

SHORT COMMUNICATIONS

J. Raptor Res. 28(3):192–193

© 1994 The Raptor Research Foundation, Inc.

PREPARATION OF AVIAN MATERIAL RECOVERED FROM PELLETS AND AS PREY REMAINS

BETH ANN SABO

*U.S. Fish and Wildlife Service, National Fish and Wildlife Forensic Laboratory, 1490 E. Main Street,
Ashland, OR 97520 U.S.A.*

ROXIE C. LAYBOURNE

*Smithsonian Institution, Division of Birds, 10th and Constitution Avenue SW,
Washington, DC 20560 U.S.A.*

KEY WORDS: *food habits technique; preparation for feather identification; prey analysis.*

Pellets and prey remains provide evidence of raptor food habits (Errington 1932, Glading et al. 1943, Collopy 1983, Marti 1987). Several researchers (Clark 1972, Longland 1985, Holt et al. 1987, Marti 1987) have addressed the “best” methods for preparing pellets to facilitate identification of contents. Because researchers have generally focused on mammal-eating raptors, methods for preparing mammalian skeletal remains prior to identification are well-defined; these techniques work equally well for avian skeletal material.

Feather material, often present in pellets and as prey remains, must be clean to be identified accurately. The cleaning process must expose original color, texture and shape of the feather. Feather material of different taxa will appear different during washing and drying, offering clues to identification. Useful techniques for handling pellets and prey remains, as well as suggestions for the preparation of avian material (feather or skeletal) prior to identification are presented below.

The dry method of pellet dissection has many advantages over other techniques (see Holt et al. 1987). No special equipment or solvent is required, and dry dissections can be accomplished in any clean and well-lighted work area. To begin, select a pellet and place it on a clean tray. Being careful not to further fragment bones or feathers, use dissection needles or forceps to gently break the pellet apart. If you meet resistance, work on another part of the pellet. Using a hand lens or dissecting microscope, separate feathers as you remove them from the pellet. In addition to whole feathers, save every bit of feather material that you find: a single barb might later provide positive identification of a prey item.

Prepare a cleaning solution by dissolving a small amount of a gentle soap (we use Ivory powder or liquid Dawn) in warm or hot tap water in a clean beaker, and add the feathers or bones to the solution. Hot water relaxes feathers and they regain their original shape. Using forceps, agitate the material in the soap solution to remove dirt and grease; when the water becomes cloudy or dirty, repeat the washing process. When changing the water, use a sieve or forceps to remove the feathers. To avoid mixing the samples, carefully clean the sieve or forceps between samples. Continue washing until the water is no longer discolored—at least two baths are generally required.

Soap film leaves a bluish or chalky cast to the feathers, and it is important to thoroughly rinse the feathers after washing. Several changes of clean, warm water may be required. When the rinse water clears, transfer the feathers to a paper towel to absorb most of the water.

To complete the cleaning process, the feathers must be dried and returned to a natural condition. Feathers not fluffed during the drying process will be clumped and misshapened when dry. Compressed air, electric fans, blow-driers, and hand driers will facilitate drying; alternatively, the feather material may be fluffed by hand. Compressed air will drive moisture out of a sample quickly, although the force associated with this source may disturb the structure of the feathers. Be cautious when first using compressed air on a sample; use short, soft bursts only. Large pennaceous feathers, such as remiges and rectrices, must carefully be blown parallel to the direction of the barbs, or the barbs will become disassociated, twisted and bent, and will not return to their original configuration. Long, downy barbs (for instance those of strigiform and falconiform birds) are susceptible to tangling, and compressed air should not be used for drying feathers from these groups. Instead, these feathers should be allowed to

air dry on paper towels and be fluffed individually by hand; hold each feather at the base of the rachis, and blow or fluff toward the tip of the feather. Small feathers can be tumbled and fluffed in a fine mesh screen basket by forcing compressed air through the screen. Clean the screen between samples.

When the recovered feathers are clean, dry, and have regained their original color and shape, they can be accurately identified. As the cleaning and drying process is mastered, the examiner will gain familiarity with feather characteristics offering clues to family, genus and species of origin. Identifications are accomplished through comparison with materials in a systematic or synoptic collection (Errington 1930, Marti 1987).

RESUMEN.—El análisis de presas remanentes y egagrópilas proveen información sobre los hábitos alimentarios de las rapaces. Nosotros recomendamos el método seco de disección de egagrópilas. Plumas y elementos del esqueleto recuperados de remanentes de presas o egagrópilas deben ser limpiados para ser identificados; estos pueden ser lavados en una solución de agua caliente con detergente suave aplicada en chorro. El material se debe agitar mientras se remoja y se lava repetidas veces. Luego, el material se enjuaga varias veces utilizando agua temperada y caliente, hasta que todo el jabón es removido. Tanto las plumas como los elementos del esqueleto son secados usando aire comprimido o secador. Las identificaciones del material desconocido son posibles al compararlos con especímenes de una colección sistemática o sinóptica.

[Traducción de Ivan Lazo]

ACKNOWLEDGMENTS

We thank Tim Mersmann, Martin Gilroy and Stephen D. Busack for critical review of this paper.

LITERATURE CITED

- CLARK, R.J. 1972. Pellets of the short-eared owl and marsh hawk compared. *J. Wildl. Manage.* 36:962-964.
- COLLOPY, M.W. 1983. A comparison of direct observations and collections of prey remains in determining the diet of golden eagles. *J. Wildl. Manage.* 47:360-368.
- ERRINGTON, P.L. 1930. The pellet analysis method of raptor food habits study. *Condor* 32:292-296.
- . 1932. Technique of raptor food habits study. *Condor* 34:75-86.
- GLADING, B., D.F. TILLOTSON AND D.M. SELLECK. 1943. Raptor pellets as indicators of food habits. *Calif. Fish Game* 29:92-120.
- HOLT, D.W., L.J. LYON AND R. HALE. 1987. Techniques for differentiating pellets of short-eared owls and northern harriers. *Condor* 89:929-931.
- LONGLAND, W.S. 1985. Comments on preparing owl pellets by boiling in NaOH. *J. Field Ornithol.* 56:277.
- MARTI, C.D. 1987. Raptor food habits studies. Pages 67-80 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird [EDS.]. Raptor management techniques manual. Natl. Wildl. Fed. Sci. Tech. Ser. No. 10, Washington, DC U.S.A.

Received 6 July 1993; accepted 28 March 1994

USE OF MIST NETS AND A LIVE GREAT HORNED OWL TO CAPTURE BREEDING AMERICAN KESTRELS

KAREN STEENHOF

*Raptor Research and Technical Assistance Center, U.S. National Biological Survey,
3948 Development Avenue, Boise, ID 83705 U.S.A.¹*

GEORGE P. CARPENTER

Raptor Research and Technical Assistance Center, Boise State University, Boise, ID 83725 U.S.A.

JAMES C. BEDNARZ

*Department of Biological Sciences, Arkansas State University, P.O. Box 599,
State University, AR 72467 U.S.A.*

KEY WORDS: *American kestrel; Falco sparverius; Idaho; mist nets; techniques; trapping.*

Many studies require that territorial adult raptors be captured safely and cost-effectively during the breeding season. Bloom (1987) and Bloom et al. (1992) reported that a dho-gaza with a great horned owl (*Bubo virginianus*) placed near the nest is the most effective way to trap small raptors during the nesting season. Mist nets have been used to capture American kestrels (*Falco sparverius*) and other raptors during migration (Clark 1970), but there have been no reports of their effectiveness for trapping breeding American kestrels. In 1993, we initiated a study of site fidelity at nest boxes in southwestern Idaho. Because we caught 75% of the adult females and only 19% of the adult males in 48 boxes during nest checks, we decided to evaluate mist nets as an alternative technique to capture breeding male kestrels.

METHODS

We tested the effectiveness of mist nets placed within 20 m (usually in front) of a nest box, with a live great horned owl tethered behind the nets (Fig. 1). We set up two 2-ply nylon 110 denier nets (6-cm mesh) at occupied nest boxes. Nets were 2.1 m high and were arranged in a v-shape around the tethered owl; one net was 5.5 m long, and the other was 9.1 m long. At one site we used a single net because various structures prevented us from using a v-shaped configuration. The lure owl was tethered with a swivel and short leash to a stake in the ground, about 1 m from the nets. Where possible, we set the trap near trees to provide shade for the nets and to minimize potential heat stress to the lure owl. We played tape recordings of a great horned owl's 5-note territorial hoot during seven of 23 trapping attempts. After setting up the nets, we watched the trap from a vehicle parked approx-

imately 100–200 m away until a bird was caught. We trapped from 26 May to 14 July 1993 and only trapped at boxes with young >5 d of age. Nestlings were aged with a photographic aging key (Griggs and Steenhof 1993).

RESULTS AND DISCUSSION

We captured 20 adult kestrels (13 males and seven females) during 23 trapping attempts at 19 boxes. The lower number of female captures was probably related to our study goals. Because we were primarily interested in capturing males (both sexes were targets at only three of 19 boxes), we usually suspended trapping immediately after the male was caught. Males were the first birds captured in 11 successful trapping attempts, and females were caught first in five attempts. These proportions did not differ significantly from random proportions ($G^2_1 = 1.17$, $P = 0.279$). Both members of the pair were captured during three trapping attempts. The male was caught first at one site, the female was caught first at another, and both birds were caught almost simultaneously at the third. Only six of 23 trapping attempts (26%) failed to catch any birds; two of these were at the same box (1 wk apart). One trapping failure occurred at the site where we set up only one of the two nets. We returned to four sites where the target bird was not captured during the initial attempt and trapped the target birds during two (50%) of our follow-up attempts. By the end of the season, we had captured at least one of our target birds at 14 of the 19 occupied boxes.

The time from when traps were set to when birds were captured ranged from 1–38 min and averaged 8.5 min (SD = 12.3) during the 10 successful trapping attempts when we recorded this information. Total time to set up, trap and process birds, and disassemble nets at a trapping site averaged 74 min (SD = 30) during 17 trapping efforts. Time spent at 12 successful trapping attempts ranged from 25–130 min and averaged 70 min. We spent an average of 85 min at five of the six boxes where we did not capture our target bird.

Probability of capturing an adult was not related to the

¹ Formerly U.S. Bureau of Land Management.

age of its young (Mann-Whitney $U = 44$, $P = 0.623$). Ages of nestlings during successful trapping attempts ranged from 6–26 d ($\bar{x} = 16$ d), and ages during failed trapping attempts ranged from 14–28 d ($\bar{x} = 18$ d). Young fledged from all of the nests where we trapped.

Capture rates were lower ($G^2_1 = 4.78$, $P = 0.029$) for trapping attempts with the tape playback than for trapping attempts without the tape. Only three of seven trapping attempts with the playback tape resulted in captures, whereas at least one kestrel was trapped in 14 of 16 trapping attempts without the tape. We used taped playbacks primarily at sites where we anticipated a low probability of success (e.g., at sites where earlier trapping attempts had failed). We believe the tape probably had no influence on whether kestrels were captured.

Most (21 of 23) of our trapping attempts occurred before noon (MDT), but both afternoon trapping attempts captured birds. Five of the six unsuccessful trapping attempts were before 0800 H, and only four of 20 birds were captured before 0800 H. We avoided trapping in the afternoon because we suspected that winds and lighting conditions would make nets more conspicuous; we also did not want to subject the lure owl to heat stress.

Only one non-target species, a western kingbird (*Tyrannus verticalis*), was captured during our trapping efforts. Swainson's hawks (*Buteo swainsoni*), eastern kingbirds (*Tyrannus tyrannus*), black-billed magpies (*Pica pica*), and long-billed curlews (*Numenius americanus*) also mobbed the lure owl.

The mist nets employed in this study were firmly attached to net poles and did not detach as dho-gaza nets do. One possible advantage of using mist nets over dho-gazas with kestrels is that nets do not need to be reset if the bird encounters the net and escapes (i.e., "bounces out") or if the dho-gaza triggers prematurely (e.g., by wind). The process of resetting a dho-gaza can disturb the target birds and may reduce the likelihood of capture. Although we did not record the number of cases that birds bounced out of our nets, it occurred only rarely during our study. When it did occur, mist nets were still in place, and kestrels were caught later during the same trapping session. The advantage of using mist nets may be nullified for larger hawks because of the increased probability that larger hawks will bounce out or escape from mist nets.

Mist nets seem to be an effective and efficient technique for capturing male American kestrels during the breeding season. Our approach eliminates the need for repeated checks of the box and probably minimizes disturbance to eggs or chicks. A live owl might be more effective than a stuffed owl because the kestrels seemed to respond to the owl's movements. Tapes of owl vocalizations did not enhance trapping success in our study. We recommend that trapping be deferred until after young are capable of thermoregulation (approximately 8 d; Balgooyen 1976) so that trapping does not keep adults from tending eggs or vulnerable young.

RESUMEN.—Usamos redes de niebla con *Bubo virginianus* como señuelos vivos, con el fin de capturar *Falco sparverius* en el suroeste del Idaho. Atrapamos 13 machos y siete hembras en 23 intentos distribuidos en 19 cajas de de captura dispuestas durante 1993. El éxito de captura no

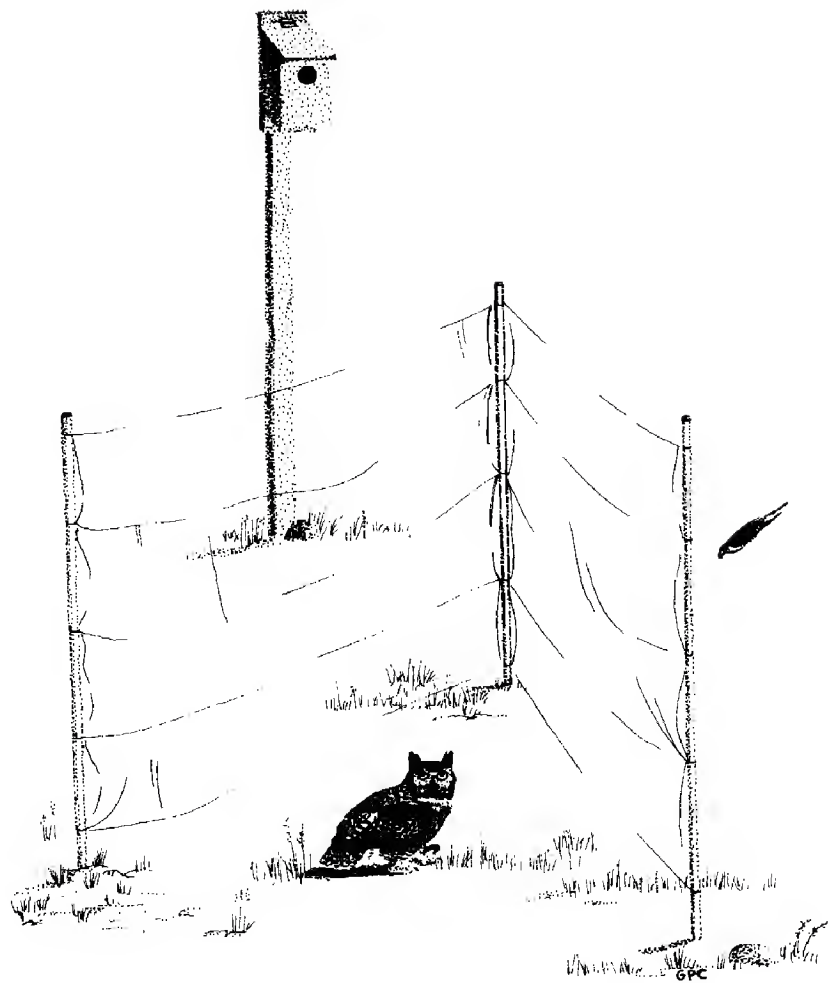


Figure 1. Configuration and placement of mist nets used to capture American kestrels in southwestern Idaho, 1993.

estuvo relacionado con la edad de los pollos, tiempo del día o si se usó vocalizaciones grabadas de *B. virginianus*. Las redes de niebla con señuelos vivos parecen ser una efectiva técnica para capturar *F. sparverius* durante la estación reproductiva.

[Traducción de Ivan Lazo]

ACKNOWLEDGMENTS

This paper is a contribution from the Raptor Research and Technical Assistance Center, U.S. Bureau of Land Management, and Boise State University. We thank Marc Bechard of Boise State University and John Hall of Zoo Boise for allowing us to use the owl. Lisa Hanke assisted with trapping efforts, and Michelle Drysdale, Andy Benolkin, Deana Parrish, and Barbara Stuart helped to find occupied nest boxes. The National Geographic Society provided a ladder for checking boxes. R. Rosenfield and P. Bloom reviewed the manuscript and offered helpful suggestions.

LITERATURE CITED

- BALGOOYEN, T.G. 1976. Behavior and ecology of the American kestrel (*Falco sparverius*) in the Sierra Nevada of California. *Univ. Calif. Publ. Zool.* 103:1–74.
BLOOM, P.H. 1987. Capturing and handling raptors. Pages 99–123 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird [Eds.], *Raptor manage-*

- ment techniques manual. Natl. Wildl. Fed., Washington, DC U.S.A.
- , J.L. HENCKEL, E.H. HENCKEL, J.F. SCHMUTZ, B. WOODBRIDGE, J.R. BRYAN, R.L. ANDERSON, P.J. DETRICH, T.L. MAECHTLE, J.O. MCKINLEY, M.D. MCCRARY, K. TITUS AND P.F. SCHEMPF. 1992. The Dho-gaza with great horned owl lure: an analysis of its effectiveness in capturing raptors. *J. Raptor Res.* 26: 167–178.
- CLARK, W.S. 1970. Migration trapping of hawks (and owls) at Cape May, NJ—third year. *EBBA News* 33: 181–189.
- GRIGGS, G.R. AND K. STEENHOF. 1993. Photographic guide for aging nestling American kestrels. U.S. Dep. Inter., Bur. Land Manage., Boise, ID U.S.A.

Received 11 February 1994; accepted 26 April 1994

LETTER

HOOK AND LOOP TABS FOR ATTACHING A DHO-GAZA

The dho-gaza has been used for capturing raptors and other birds for hundreds of years (R.L. Meredith 1943, *Methods, ancient, medieval, and modern, for the capture of falcons and other birds of prey*. Pages 433–449 in C.A. Woods and F.M. Fyfe [EDS.], *The art of falconry*. Stanford Univ. Press, Stanford, CA U.S.A.). Each set typically consists of a small net usually not larger than 3 × 3 m. Netting may consist of a fine mist net or a heavier type net which will break away from or slide down its supporting poles when hit by a passing bird (P.H. Bloom 1987, *Capturing and handling raptors*. Pages 99–123 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline and D.M. Bird [EDS.], *Raptor management techniques manual*. Natl. Wildl. Fed., Washington, DC U.S.A.; H. Bub 1991, *Bird trapping and bird banding*. Cornell Univ. Press, Ithaca, NY U.S.A.). Cellophane tape and clothes pins (P.H. Bloom 1987, *Capturing and handling raptors*. Pages 99–123 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline and D.M. Bird [EDS.], *Raptor management techniques manual*. Natl. Wildl. Fed., Washington, DC U.S.A.; H. Bub 1991, *Bird trapping and bird banding*. Cornell Univ. Press, Ithaca, NY U.S.A.) or small wires (F. Hamerstrom 1963, *The use of great horned owls in catching marsh hawks*. *Proc. Int. Ornithol. Congr.* 13:866–869) are the most common methods of attaching a net to the poles.

We found fabric hook and loop fasteners, such as Velcro®, to be superior to the more commonly used methods of suspension (Fig. 1). At each corner of the net, a 1.3 × 6 cm strip of the loop side of self-adhesive Velcro is folded in half around the trammel line forming a tab 3 cm long (Fig. 1). We then attached 10-cm strips of the corresponding hook side of the Velcro to each pole at the approximate positions necessary for hanging the net (Fig. 1). In a recent article by D. Rasmussen (1991, *Hawk Chalk* 30:60–64), a Velcro tab is mentioned as a means of anchoring a dho-gaza release line, but not for attaching the net to the poles.

Attaching the loop side of the Velcro to the net, rather than the pole, minimizes entanglement with the net. Once the poles are anchored in place, attachment of the net is simple and expedient. After numerous uses, Velcro may need to be replaced because it may lose its tensile strength or become fouled with debris.

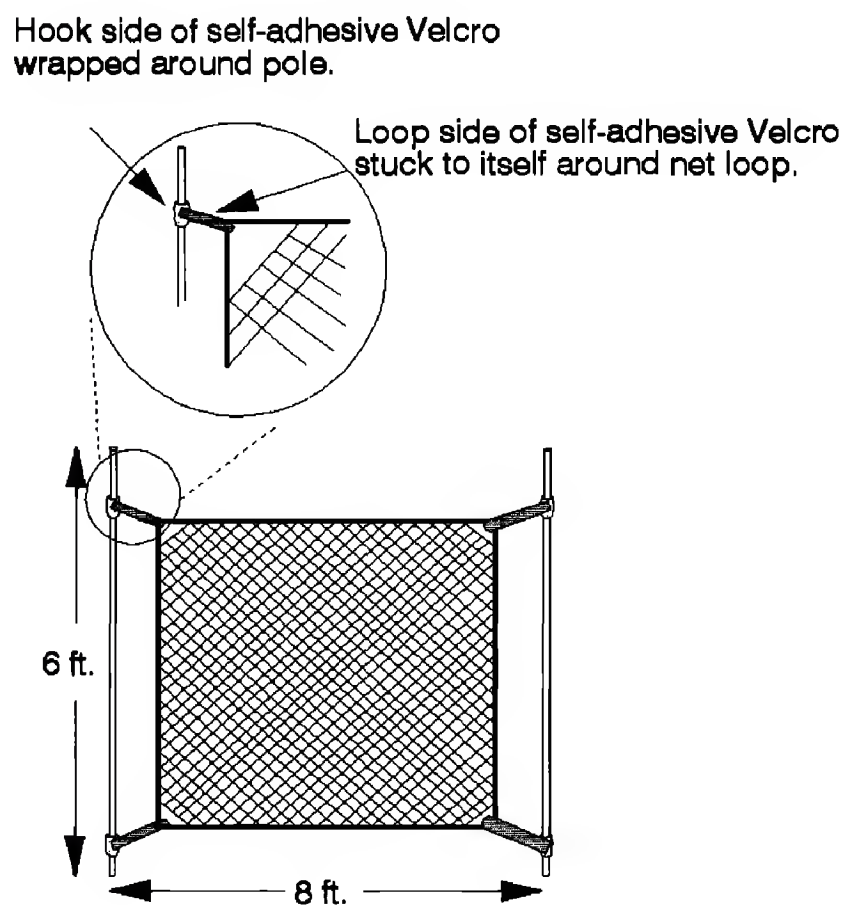


Figure 1. Dho-gaza set showing use of Velcro tabs as restraints for net to poles.

The Velcro tabs allow for simple adjustments to wind and trapping conditions by varying the amount of surface contact between the net tabs and the tabs on the poles. The net can also be firmly attached to the poles for cleaning and damage repair. We have used this method to capture several species of birds including common ravens (*Corvus corax*), northern harriers (*Circus cyaneus*), and Cooper's hawks (*Accipiter cooperii*).

The modification of this raptor capture device was a small part of a research project funded by the United States Department of Defense, U.S. Naval Surface Forces, Pacific Command, on behalf of the Assault Craft Unit-Five and the Landing Craft Air Cushion Program at Camp Pendleton Marine Base, California.—**C. Edward Knittle, USDA/Denver Wildlife Research Center, Building 16, Federal Center, Denver, CO 80225 U.S.A. and Mark A. Pavelka, United States Fish and Wildlife Service, 2730 Loker Avenue West, Carlsbad, CA 92008 U.S.A.**

BOOK REVIEWS

EDITED BY JEFFREY S. MARKS

J Raptor Res. 28(3):199–200

The Mississippi Kite: Portrait of a Southern Hawk. By Eric G. Bolen and Dan Flores. 1993. University of Texas Press, Austin, Texas. xi + 115 pp., 14 color plates, 3 figures, 2 tables, 3 appendices. ISBN 0-292-75148-6. Cloth, \$17.95.—According to the authors, this book was written because of the Mississippi kite's (*Ictinia mississippiensis*) aesthetic value and as a reminder to readers of the importance of predators to the natural order. An additional goal of the book was to demonstrate that an ecologist and an historian could jointly produce a useful book.

The book begins with an historical account of the first Mississippi kite described in 1806 at Natchitoches, Louisiana by Peter Custis. The authors then describe the Mississippi kite by relating an experience with several kites soaring overhead in west Texas. Personal experiences such as this are integrated throughout the book and serve to enhance its overall readability. Common names assigned to the Mississippi kite in specific parts of its breeding range in the southern United States are provided. Mention is given to the confusion that arises when several different local names are used for the same species. No mention is made of local names assigned to kites on their wintering grounds, however.

The breeding range of the Mississippi kite in North America is clearly illustrated by two maps, one of which shows the bird's westward range expansion in recent years. The authors attempt to integrate other raptors into their explanations and descriptions and thus do not restrict their accounts to Mississippi kites. For example, species such as the peregrine falcon (*Falco peregrinus*), snail kite (*Rostrhamus sociabilis*), and American swallow-tailed kite (*Elanoides forficatus*) are also discussed.

A chapter entitled "Mississippi Kites in History" includes interesting accounts of kites written by nineteenth century western explorers. Specific experiences by such famous naturalists as John James Audubon and Alexander Wilson provide excellent examples of the attitudes toward predators during

that period. The chapter closes with a report on the kites' responses to recent environmental changes, especially those related to shelterbelts. The authors make the point that, due to shelterbelt plantings in the southern High Plains, Mississippi kites now thrive in large colonies not seen by early western explorers.

Mississippi kite migration patterns from their Neotropical wintering grounds to their North American breeding grounds are described. The authors propose three migration routes for the kites but conclude that the overland route through Central America is the one used most commonly.

Breeding biology, including courtship, nest-site selection, clutch size, egg characteristics, incubation, nest defense, and colonial nesting is described. The color plates in this chapter are of excellent quality and enhance the text considerably.

Parental care is considered briefly along with a short discussion on nest helpers. Examples of reproductive success (percentage of eggs hatched and number of young raised per successful nest) in three habitats are reported in a table. A major drawback here is the lack of a clear source for the data used to construct the table. The kite's typical habit of fiercely attacking predators in the vicinity of nests, while allowing conspecifics to remain unmolested, is included along with comments on gregarious behavior.

Feeding behavior is described in some detail. Interesting personal accounts of kites feeding on swarming cicadas (the main food source during the breeding season) are included. Using Snyder and Wiley's dimorphism index, sexual size dimorphism is compared with other raptor species. Measurements of wing chord, bill length, and body mass for both male and female kites are provided in a table. The source of the data, while alluded to in the text, is not provided in the table.

The increasing frequency of large breeding colonies of kites in urban settings (e.g., Clovis, NM and Garden City, KS) is the focus of the next chapter. The problem of kites nesting on golf courses and diving upon anyone near their nest trees is described.

The authors stress that aerial dive-bombing by kites rarely results in injuries to people—on a golf course in New Mexico, 900 attacks resulted in strikes only 3% of the time.

The relationship between predators and people is described using both historical and ecological accounts. The mass slaughter of raptors at Hawk Mountain in the early part of this century is described in the text and depicted in a photograph of several raptors killed by hunters. Bounties offered by several states in the early part of this century are blamed for the deaths of large numbers of raptors. The idea that predators remain hungry most of the time and “rarely live up to their reputations as efficient killers” is stressed. The value of raptors as agents of pest control is provided as one justification for their protection. The loss of raptor eggs and nestlings to “overzealous” egg and specimen collectors is described with reference to detailed (and sometimes gruesome) accounts from the older literature.

Problems with the survival of many species of Neotropical migrants while on their wintering grounds have become the focus of much concern. The authors attribute a majority of these problems to deforestation and use of pesticides by several Neotropical countries. The effects of pesticides and deforestation on wintering Mississippi kites, however, are not well understood. The establishment of protected areas throughout the kite’s breeding range in southern North America is suggested as a way to mollify potential problems faced by the kites on their wintering grounds.

The book contains three appendices. The first lists scientific names of the species discussed in the text. The second describes Snyder and Wiley’s dimorphism index in detail and provides the equation used to calculate the dimorphism index for Mississippi kites. The third appendix lists Mississippi kite sightings during the last 10 yr by each state reporting such sightings. Suggested readings and references are provided both in general and by chapter at the end of the book.

The strong points of this book are many. It provides interesting and entertaining reading, and the color plates are excellent and effective. The wealth of information presented makes the book suitable for bird watchers, amateur and professional naturalists, and ornithologists. The information contained in the book far outweighs its size and reflects the amount of time spent by the authors in uncovering interesting

details, especially historical accounts of the species. An unfortunate shortcoming of the book is a failure to provide citations for data contained in the text and tables. Nonetheless, I recommend this book as an excellent starting place for those beginning research on Mississippi kites and for anyone interested or inspired to learn more about them. This book is especially suitable for both public and university libraries.—**Eugene S. Botelho, Department of Biology, New Mexico State University, Las Cruces, NM 88003-0001 U.S.A.**

J. Raptor Res. 28(3):200–201

Las Rapaces Ibericas. By J.L.G. Grande and F. Hiraldo. 1993. Aldaba Ediciones, S.A., Spain. 295 pp., more than 290 color photos, 1 color plate, 32 range maps. ISBN 84-86629-73-X (In Spanish). Cloth, no price given.—This is basically a book out of the same genre as *Eagles, Hawks and Falcons of Australia* by David Hollands. Although this book on “The Raptors of Spain” is also principally a book emphasizing photographs, it nonetheless lacks the scientific rigor of the Hollands tome. The photographs are of high quality. Each species is shown in flight, and many are also shown in a nesting setting and with typical prey. It would largely be in vain to try and single out exceptional photographs, but there are especially excellent ones of the griffon vulture (*Gyps fulvus*) and the imperial eagle (*Aquila heliaca*), for example. In all, 25 diurnal raptors and seven owls are treated as occurring in Spain.

As with most books of this type, the treatment of each species varies with the amount of data available. One extensively treated species is the imperial eagle, with section headings on “The Species and its Morphological Characteristics,” “Population and Distribution,” “Habits,” “Feeding and Foods,” “Reproduction,” and “Conservation Problems.” On the other hand, the long-eared owl (*Asio otus*) represents the more average species account and contains only introductory material and sections on “Distribution,” “Population and Habitat,” “Food,” and “Reproduction.”

The distribution maps include the Balearic Is-

lands (three major islands just east of Spain), but to my disappointment, not the Canary Islands, which are also a possession of Spain (but situated off the coast of Morocco). This is unfortunate because both island groups have some curious distributions. Much of the distribution on the islands is a function of the presence of cliffs or other appropriate habitats and thus emphasizes differences among islands. For example, the scops owl (*Otus scops*) occurs on all of the Balearics, whereas the little owl (*Athene noctua*), which is generally as broadly distributed as the scops owl, is absent. Likewise, the barn owl (*Tyto alba*) occurs on two of the three islands, but the long-eared owl on only one of them. This same sort of "fragmented distribution" in raptors occurs on the Canary Islands, and it would have been nice to have shown that.

Overall, this is a great book to have for one's library simply because of the photographs, if for no other reason. I highly recommend it even for those who do not read Spanish. The title page is one of encouragement with the statement "All Birds of Prey are Protected by Law in Spanish Territory by Royal Decree No. 3181, 30 December 1980. Juan Carlos de Borbon, King of Spain" (my translation).—**Clayton M. White, Department of Zoology, Brigham Young University, Provo, UT 84602 U.S.A.**

J Raptor Res. 28(3):201–203

Barn Owls: Predator-Prey Relationships and Conservation. By Iain Taylor. 1994. Cambridge University Press, Cambridge, England. xvi + 304 pp., 119 figures, 15 tables, 3 appendices. ISBN 0-521-39290-X. Cloth, \$37.95.—The barn owl (*Tyto alba*) is by far the most well-studied owl in the world. Iain Taylor has added to this bank of knowledge with his long-term study of the nominate race, *T. a. alba*, in southern Scotland. This book is based largely on his personal experiences with these owls. It is written for "researchers, professionals and interested amateurs." The underlying theme is that a thorough understanding of the relationship between predators and their prey is essential to effective conservation efforts. Recognizing that not all facets of the owl's

ecology are directly related to food, however, Taylor also addresses other important life-history attributes. Throughout the book, he compares his findings with those from studies in mainland Europe and from other continents. The result is a well-balanced treatment of the autecology of barn owls.

Each chapter begins with an attractive drawing by Keith Brockie, and all but the final chapter ("Conclusions") end with a concise summary. Chapter 1 presents a brief introduction to the species, descriptions of the four study areas, and a general overview of study methods. The main study site (1600 km²) was centered around the River Esk and its tributaries. Within this area Taylor strived to locate all nests initiated from 1978 to 1992, subsequently trapping and measuring the adults and banding all of the young produced. He also monitored food habits, censused small mammals, and radio-tagged 10 breeding pairs.

Chapter 2, entitled "Distribution and Variation," contains a map showing the distribution of the 36 subspecies of barn owls. Focusing on the *alba* subspecies, Taylor describes and depicts plumage differences between the sexes. Compared with males, females are more richly colored and have more markings on their wings, tail, and venter. They become paler with age, however, such that those ≥ 7 yr old may be as pale as males. Mensural data from 22 subspecies (presented in Appendix 1) reveal substantial intraspecific variation in size. The *javanica* subspecies from Southeast Asia is by far the largest in mass, followed by *pratincola* from North America. The former has shorter wings, however, and hunts more from perches than in flight. The tropical subspecies tend to have longer tarsi, which Taylor suggests is an adaptation for prey capture in tall grasses that are common at lower latitudes. Within subspecies, there is little difference in size between the sexes except that males weigh less than females. Consequently, males should have lighter wing-loading, a point that Taylor neglects to mention. Indeed, there is no discussion of the adaptive significance of sexual size dimorphism (or lack thereof) in barn owls.

Diet and foraging behavior are the topics of Chapters 3 and 4. A summary of 52 studies confirms that mammals are the main prey, constituting 74–100% of the diets. Voles (*Microtus*) dominate the diets in western Europe and North America, whereas mice (*Mus* and *Apodemus*) predominate in Mediterranean climates. Taylor dislikes diversity indices because of their "disadvantages," yet he does not specify these

drawbacks. As an alternative, he calculates the minimum number of prey species needed to make up 80% of the diet. This seems like a reasonable (albeit arbitrary) index of dietary diversity, but I do not see how it is any better than the inverse of Simpson's index or the antilog of Shannon's index.

Thinking that barn owls were almost exclusively active-search foragers, I was surprised to learn that perch-hunting has been observed in many places. Indeed, it is the main foraging technique of barn owls in Malaysia. An interesting exception to the notion that barn owls are strictly nocturnal comes from Scotland and northern England, where they "quite normally hunt during the day" in both winter and summer. Taylor offers the novel suggestion that the white plumage of male *alba* (which is the palest subspecies) could function to reduce conspicuousness of diurnally foraging owls to their prey (p. 51). This may be so, but one wonders how well a vole can see a foraging owl, even in daylight. Moreover, it cannot explain why North American barn owls (which are nocturnal) are also pale. It strikes me that more than any other owl, barn owls nest and roost in sites that are particularly well concealed. Perhaps they are pale simply because they do not require the cryptic plumage typical of species that nest and roost in more open situations.

Taylor presents a succinct review of the behavior and ecology of the prey species in Chapter 5. As such, he sets the stage for subsequent discussions of predator-prey relationships. Trapping data show how the abundance of prey varies seasonally and from year to year. They also reveal that moist grassland habitats preferred by voles in Scotland are restricted to the edges of grazed pastures, farmlands, and fence-rows. An unfortunate trend that begins in this chapter (and continues through the literature citations) is the misspelling of the last name of noted owl researcher Erkki Korpimäki.

Chapter 6 is entitled "Prey Selection, Foraging Habitats and Energetics." It begins with a useful review of several field studies that have suggested that barn owls prefer voles over other available species (mostly mice). Two experiments with captive owls corroborate this preference. Taylor suggests that voles are larger and easier to catch than mice and are thus more profitable prey for barn owls.

The section on energetics reviews estimates of food intake and energy consumption measured in captive owls. The thermal neutral zone of barn owls is higher than that of other owls, suggesting that they are

adapted to relatively warm climates. This explains their habit of roosting in buildings and cavities during daytime and of "resting" in buildings between foraging bouts at night. The fact that many owls died during a period of prolonged cold and snow in Scotland suggests that barn owls have difficulty meeting daily food requirements at the northern edge of their range.

Data in "Ranging and Roosting Behaviour" (Chapter 7) are based largely on radio-tagged owls. Home range size was measured for six breeding pairs during a low vole year (1983) and four (see below) during a high vole year (1984). Data are presented for 1983 but not for 1984. Thus, there is no support for the statement that home range sizes were equal in both low and high vole years (p. 100). Moreover, the number of pairs tracked in 1984 is said to be four on p. 98 and five on p. 101. This inconsistency, and the lack of data for all pairs tracked, mars an otherwise interesting account of breeding-season movements.

Taylor spent considerable time watching his radio-tagged birds. Thus, in addition to documenting that foraging areas of adjacent pairs overlapped considerably, he discovered that the owls did not defend feeding territories. Rather, they confined their attacks to intruders that entered occupied nest sites.

Chapter 8 examines molt. Scottish barn owls have the same complex molt patterns documented in mainland Europe and the United States. Complete replacement of the juvenal primaries occurs over a 3-yr period beginning with one or two primaries during the owl's second calendar year. Owls ≥ 5 yr old replace their primaries on a 2-yr cycle, beginning with P6 and progressing in both directions in small blocks of adjacent feathers. About 25% of the females begin shedding primaries during incubation, whereas males do not begin molt until the young are nearly full grown. More females overlap molt with incubation during high vole years than during low vole years, indicating food-based plasticity in energy allocation. Interestingly, barn owls in Malaysia exhibit the same sequence of primary molt as temperate birds but complete the entire molt over a 7-mo period.

Various aspects of breeding biology are covered in Chapters 9 through 12. Laden with information, these chapters contain the meat of Taylor's research. Not surprisingly, the vole cycle influences a variety of reproductive traits including laying date, renesting effort, clutch size, nesting success, and survival of

young. There is also a strong influence of age on timing of nesting, with yearling females laying substantially later than older females. In addition, during high vole years when many yearlings breed, yearling females tend to pair with yearling males.

Taylor states that barn owls do not construct nests. This contradicts several published studies (dating back to the late 19th century) that have documented burrow digging by barn owls in the United States (e.g., Martin 1973, Millsap and Millsap 1987). This minor oversight detracts little from an otherwise thorough review of barn owl nesting sites.

The data on dispersal (Chapter 13) are perhaps the best available for the species. They show that adults are highly faithful to previous breeding sites and that most young settle within 10 km of their natal sites. There is a slight but significant trend for males to settle closer to their natal sites than do females. No cases of close inbreeding were observed.

There was no evidence that Scottish barn owls were migratory. Perhaps for this reason, Taylor is skeptical of reports of barn owl migration in the United States. He suggests that "migratory" barn owls observed at Cape May, NJ were actually dispersing juveniles. Yet, in both Colorado and New Jersey, researchers have documented southward movements by adults (Millsap and Millsap 1987, Duffy and Kerlinger 1992).

Chapters 14 and 15 treat mortality and population regulation, respectively. Annual mortality ranged from 16–55% per year for adults and was closely tied to vole abundance. Similarly, there was a strong positive correlation between vole numbers and the number of nesting pairs each year. Taylor concludes that the upper limit of nesting density is controlled by a combination of prey abundance and availability of suitable nesting sites.

In Chapter 16, Taylor discusses the population declines of barn owls in Europe and the United States that apparently began in the 1930s and 1940s. He also offers some insightful thoughts on conservation via management of foraging habitats, provisioning of nest sites, and control of rodenticide use. This chapter should be required reading for anyone contemplating a management program for raptors. The final chapter is a useful and well-organized summary of the book.

On balance, I liked the book very much. It is attractively produced, reasonably priced, relatively free of typographic errors (I noted only two), and packed with original data. The review of information from other continents enhances the book's value. As a minor criticism, I think that Taylor could have gone further in suggesting avenues for additional research. Nonetheless, the careful reader should have no trouble identifying gaps in present knowledge and devising interesting research questions. *Barn Owls* should be acquired by all university libraries and anyone with a specific interest in *Tyto alba*. It should also be read by anyone interested in long-term studies of raptor populations.—**Jeff Marks, Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812 U.S.A.**

LITERATURE CITED

- DUFFY, K. AND P. KERLINGER. 1992. Autumn owl migration at Cape May Point, New Jersey. *Wilson Bull.* 104:312–320.
- MARTIN, D.J. 1973. Burrow digging by barn owls. *Bird-Banding* 44:59–60.
- MILLSAP, B.A. AND P.A. MILLSAP. 1987. Burrow nesting by common barn-owls in north central Colorado. *Condor* 89:668–670.

IN MEMORIAM
RICHARD R. OLENDORFF
1943–1994

The raptor research community lost one of its leading and most beloved members recently. On 24 February 1994, Dr. Richard R. "Butch" Olendorff died of complications from diabetes at the age of 50.

Butch was a charter member of the Raptor Research Foundation (RRF) and served as editor of the *Journal of Raptor Research* from 1971–76, secretary of the RRF from 1975–1976, and president from 1977–1981. He also served on the RRF Board of Directors from 1975–1977, and from 1980–1982. In 1991, the RRF honored Butch with its most prestigious award, the President's Award, and the 1994 RRF annual meeting will be dedicated to Butch's memory.

Butch received the B.S. degree in zoology from the University of Washington in 1967, and completed a Ph.D. at Colorado State University in 1971. Between 1971 and 1974, he was a Post-doctoral Fellow and Research Associate at the American Museum of Natural History in New York. In 1974, he joined the U.S. Bureau of Land Management (BLM) as Endangered Species Liaison Officer in Washington, DC. From 1977–1989, Butch served as the Endangered Species Coordinator in the BLM California State Office in Sacramento. In 1989, Butch moved to Boise, Idaho to establish the Raptor Research and Technical Assistance Center, now a unit of the National Biological Survey.

Butch's love of raptors came to him early. He took up falconry at the age of 15, and was a founding member of the North American Falconers Association. He quit flying his birds only when the demands of his profession became too great. For his post-doctoral research he studied prairie raptors in the Pawnee National Grasslands of northeastern Colorado where, he often said, he found his spiritual home among the buttes. His work there led to a number of published papers and a book, *Golden Eagle Country*, about raptors and the problems confronting them. In addition to his regular duties with BLM, Butch found time to write a number of state-of-the-art papers concerning raptors, and during his professional life produced over 35 publications. During the 1980s, he developed a computerized bibliography on raptor management with over 10 000 references. In 1985, he conceived of and was instrumental in organizing the World Raptor Meetings in Sacramento, California, the largest such event in the history of the raptor profession.

Those of us who were close to him in his last days will remember the dignity with which Butch faced the illness that finally took him, and his determination to continue his work. He was at his desk until a few days before his final trip to the hospital working on a revision of his well-known paper "Suggested Practices for Raptor Protection on Powerlines." A few months before his death, he published his last major work, an exhaustive review of the ferruginous hawk literature.

It may be for his boundless energy and lifetime commitment to raptor conservation that Butch will most be remembered, but all who knew him will also remember Butch for his kindness, sense of humor, and deep personal integrity. Butch was scrupulously fair and examined all sides of every issue. Throughout his professional life he was respected for the courtesy he showed everyone regardless of which side of an issue they were on. He had the rare ability to recognize the values of others without passing judgment, perhaps accounting for his ability to bring people together to work toward common goals. He was direct and unflinching in his assessments of both people and issues but he was never mean-spirited. In a very real sense, Butch set the standards of personal and professional behavior that guided the raptor profession through its early years.—**Robert Lehman, National Biological Survey, Boise, ID 83705 U.S.A.**

Butch Olendorff Memorial Library. The Raptor Research and Technical Assistance Center (RRTAC) will establish the Butch Olendorff Memorial Library to house Butch's professional papers and as a center for bibliographic research on raptors when RRTAC moves to Boise State University in 1995. Memorials to fund the library may be made to the Butch Olendorff Memorial Fund, % West One Bank, Skyway Branch, 2730 Airport Way, Boise, ID 83705 U.S.A.

Butch Olendorff Lifetime Achievement Award for Conservation of Birds of Prey. The U.S. Bureau of Land Management has established the Butch Olendorff Lifetime Achievement Award for Conservation of Birds of Prey, an occasional award to recognize individuals and organizations that make remarkable contributions or sacrifices to raptor conservation. The first two recipients were Idaho Governor Cecil Andrus and Morley Nelson, both of whom were extremely influential in establishing the Snake River Birds of Prey National Conservation Area.

THE RAPTOR RESEARCH FOUNDATION, INC.
(FOUNDED 1966)

OFFICERS

PRESIDENT: MICHAEL W. COLLOPY
VICE-PRESIDENT: DAVID M. BIRD

SECRETARY: BETSY HANCOCK
TREASURER: JIM FITZPATRICK

BOARD OF DIRECTORS

EASTERN DIRECTOR: BRIAN A. MILLSAP
CENTRAL DIRECTOR: THOMAS NICHOLLS
MOUNTAIN & PACIFIC DIRECTOR:
KAREN STEENHOF
CANADIAN DIRECTOR: PAUL C. JAMES
INTERNATIONAL DIRECTOR #1:
JEMIMA PARRY-JONES

INTERNATIONAL DIRECTOR #2:
M. ISABEL BELLOCQ
DIRECTOR AT LARGE #1: JIM BEDNARZ
DIRECTOR AT LARGE #2: ROBERT E. KENWARD
DIRECTOR AT LARGE #3: KEITH L. BILDSTEIN
DIRECTOR AT LARGE #4: JOSEF K. SCHMUTZ
DIRECTOR AT LARGE #5: PAUL F. STEBLEIN
DIRECTOR AT LARGE #6: KATHERINE MCKEEVER

EDITORIAL STAFF

JOURNAL EDITOR: CARL D. MARTI, Department of Zoology, Weber State University, Ogden, UT
84408-2505 U.S.A.

ASSOCIATE EDITORS

KEITH L. BILDSTEIN
GARY R. BORTOLOTTI
CHARLES J. HENNY

FABIAN JAKSIĆ
PATRICIA L. KENNEDY
ERKKI KORPIMÄKI

BOOK REVIEW EDITOR: JEFFREY S. MARKS

EDITOR OF RRF KETTLE: RICHARD J. CLARK

The Journal of Raptor Research is distributed quarterly to all current members. Original manuscripts dealing with the biology and conservation of diurnal and nocturnal birds of prey are welcomed from throughout the world, but must be written in English. Submissions can be in the form of research articles, letters to the editor, thesis abstracts and book reviews. Contributors should submit a typewritten original and three copies to the Editor. All submissions must be typewritten and double-spaced on one side of 216 × 278 mm (8½ × 11 in.) or standard international, white, bond paper, with 25 mm (1 in.) margins. The cover page should contain a title, the author's full name(s) and address(es). Name and address should be centered on the cover page. If the current address is different, indicate this via a footnote. A short version of the title, not exceeding 35 characters, should be provided for a running head. An abstract of about 250 words should accompany all research articles on a separate page.

Tables, one to a page, should be double-spaced throughout and be assigned consecutive Arabic numerals. Collect all figure legends on a separate page. Each illustration should be centered on a single page and be no smaller than final size and no larger than twice final size. The name of the author(s) and figure number, assigned consecutively using Arabic numerals, should be pencilled on the back of each figure.

Names for birds should follow the A.O.U. Checklist of North American Birds (6th ed., 1983) or another authoritative source for other regions. Subspecific identification should be cited only when pertinent to the material presented. Metric units should be used for all measurements. Use the 24-hour clock (e.g., 0830 H and 2030 H) and "continental" dating (e.g., 1 January 1990).

Refer to a recent issue of the journal for details in format. Explicit instructions and publication policy are outlined in "Information for contributors," *J. Raptor Res.*, Vol. 27(4), and are available from the editor.

1994 ANNUAL MEETING

The Raptor Research Foundation, Inc. 1994 annual meeting will be held on 3–6 November at the Little America Hotel in Flagstaff, Arizona. Details about the meeting and a call for papers will be mailed to Foundation members in the summer, and can be obtained from Dan Varland, Scientific Program Chairperson, ITT Rayonier, Inc., Northwest Forest Resources, P.O. Box 200, Hoquiam, WA 98550, (telephone 206 533-7000), and Patricia Hall, Local Chairperson, 436 E. David Drive, Flagstaff, AZ 86011 U.S.A. (telephone 602 774-0041). For information about the associated symposia contact: Susi MacVean (northern goshawk), Arizona Game and Fish Department, 2222 W. Greenway Road, Phoenix, AZ 85023 U.S.A. (telephone 602 789-3581); Joseph Ganey (Mexican spotted owl), USDA Forest Service, Rocky Mountain Forest and Range Research Station, 2500 Pine Knoll Drive, Flagstaff, AZ 86011 U.S.A. (telephone 602 556-2156); Michael Fry (Swainson's hawk), Department of Avian Science, University of California, Davis, CA 95616 U.S.A. (telephone 916 752-1201).

RAPTOR RESEARCH FOUNDATION, INC., AWARDS Recognition for Significant Contributions¹

- The **Dean Amadon Award** recognizes an individual who has made significant contributions in the field of systematics or distribution of raptors. Contact: **Dr. Clayton White, 161 WIDB, Department of Zoology, Brigham Young University, Provo, UT 84602 U.S.A.** Deadline August 15.
- The **Tom Cade Award** recognizes an individual who has made significant advances in the area of captive propagation and reintroduction of raptors. Contact: **Dr. Brian Walton, Predatory Bird Research Group, Lower Quarry, University of California, Santa Cruz, CA 95064 U.S.A.** Deadline: August 15.
- The **Fran and Frederick Hamerstrom Award** recognizes an individual who has contributed significantly to the understanding of raptor ecology and natural history. Contact: **Dr. David E. Andersen, Department of Fisheries and Wildlife, 200 Hodson Hall, 1980 Folwell Avenue, University of Minnesota, St. Paul, MN 55108 U.S.A.** Deadline: August 15.

Recognition and Travel Assistance

- The **James R. Koplin Travel Award** is given to a student who is the senior author of the paper to be presented at the meeting for which travel funds are requested. Contact: **Dr. Petra Wood, West Virginia Cooperative Fish and Wildlife Research Unit, P.O. Box 6125, Percival Hall, Room 333, Morgantown, WV 26506-6125 U.S.A.** Deadline: Deadline established for conference paper abstracts.
- The **William C. Andersen Memorial Award** is given to the student who presents the best paper at the annual Raptor Research Foundation Meeting. Contact: **Ms. Laurie Goodrich, Hawk Mountain Sanctuary, Rural Route 2, Box 191, Kempton, PA 19529-9449 U.S.A.** Deadline: Deadline established for meeting paper abstracts.

Grants²

- The **Stephen R. Tully Memorial Grant** for \$500 is given to support research, management and conservation of raptors, especially to students and amateurs with limited access to alternative funding. Contact: **Alan Jenkins, George Miksch Sutton Avian Research Center, Inc., P.O. Box 2007, Bartlesville, OK 74005-2007 U.S.A.** Deadline: September 10.
- The **Leslie Brown Memorial Grant** for \$500–\$1,000 is given to support research and/or the dissemination of information on raptors, especially to individuals carrying out work in Africa. Contact: **Dr. Jeffrey L. Lincer, 9384 Hito Court, San Diego, CA 92129-4901 U.S.A.** Deadline: September 15.

¹ Nominations should include: (1) the name, title and address of both nominee and nominator, (2) the names of three persons qualified to evaluate the nominee's scientific contribution, (3) a brief (one page) summary of the scientific contribution of the nominee.

² Send 5 copies of a proposal (≤5 pages) describing the applicant's background, study goals and methods, anticipated budget, and other funding.